

AUSTRALIA NATURAL HISTORY

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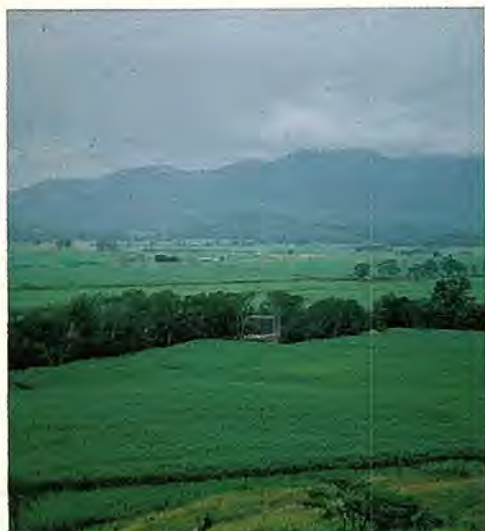
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Above, a typical scene of the rural landscape of vegetated rocky ridges surrounded by valleys and plains that have been intensively modified by agricultural practices. Part of the sugar cane country of northern Queensland with native vegetation restricted to the narrow banks of a small winding stream and the distant cloud-shrouded mountains. In the foreground a community of introduced species and fire-tolerant native grasses has become established, as they can survive the regular burning of the sugar cane. Photo Surrey Jacobs.



Pentoxylon australica leaves which are part of the find from the Talbragar Fish Beds in central NSW. Fossil evidence from this site shows the existence of a kauri pine forest 150 million years ago. Photo David Barnes.

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The editors welcome articles or photographs in any field of natural history.

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FROM THE INSIDE



Plant survival in bushfires is due to some live tissues, capable of initiating fresh growth, being shielded from the lethal temperatures generated. Protection of these tissues is interdependent on the plant's anatomy, morphology and fire intensity and must be sufficient to prevent cells experiencing temperatures of about 60°C or more for longer than a couple of minutes. Photo A. Jelinek, courtesy of the NSW National Parks and Wildlife.

Much has been written in the past on the flora of this continent, but with our rapidly expanding knowledge and constantly changing ideas on the world's floral relationships, most of this information conveys a lot of misconceptions. In this special issue of Australian Natural History we hope that we can fill part of that gap and provide the basis for a better understanding of Australia's plants and vegetation and the complex biology surrounding them.

The articles are written by experts in their respective areas of botany and cover the characteristics of our plants, the intricate processes involved in pollination, the important fossil finds from the Talbragar Fish Beds and the effects of continental drift, fire, climate and man on our flora.

While Australia is known as a land full of eucalypts, she-oaks and many different species of wattle and native heaths, the country boasts many other types of flora exhibiting a number of unusual features.

Many of our native plants have affinities with the flora of other southern continents as witnessed by the family Proteaceae, which we share with southern Africa and South America and is featured in the 'In Focus' section of the magazine. One of our oldest recognisable plant families, Proteaceae include the famous waratahs, banksias and even the inimitable macadamia nut.

With two-thirds of Australia being semi-arid to arid and the country's reputation as the world's driest continent being uppermost in peoples' minds, the importance of our rainforest and alpine flora tends to be overlooked. Australia has a series of rainforests scattered down the eastern coastal fringe from Cape York Peninsula in the tropics to Tasmania in the cool temperate zone, each containing a number of flowering plants which are known nowhere else in the world. As well as rainforests Australia also contains a significant alpine flora covering the small proportion of high country in the south-east of the continent.

With Sydney playing host to the 13th International Botanical Congress during the last half of August and attracting some 3,500 Australian and overseas delegates from 64 countries, including China and Russia, it is a particularly opportune time to focus attention on our distinctive flora.

Roland Hughes
Editor



MAN'S IMPACT ON NATIVE VEGETATION

From trouser cuff to aerial spraying, from dingo to merino, from suburban garden to rolling wheatfield, human impact on Australian flora and vegetation has had some startling results. Surrey Jacobs studied agriculture and is now a botanist at the National Herbarium of New South Wales, Royal Botanic Gardens, Sydney. He believes that humans have had an irreversible influence on our flora and vegetation and that most of these influences have occurred during the past 200 years. Surrey Jacobs research interests are in the grasses (Gramineae), chenopods (Chenopodiaceae) and aquatic plants, all of which play a dominant role in man's influences on native plants.

by Surrey W. L. Jacobs



Above, a characteristic view of the plains country of western New South Wales. The land was originally cleared to leave scattered trees for shade and sources of drought fodder. Cultivation prevents the regeneration of seedlings and the large trees gradually succumb to age, leaving ever-thinning remnants of the original vegetation. Photo: Surrey Jacobs.

Man is producing a rural landscape of vegetated rocky ridges surrounded by valleys and plains that have been intensively modified by agricultural practices. In areas where ridges are absent, refuges for native species are rapidly diminishing. The ridges themselves are increasingly under assault in many areas from suburbia and mining, and as sources of timber and rough grazing.

Man's attack on the native vegetation has been two-pronged, firstly by alteration of habitats, making them unsuitable for many of the native species previously growing there and secondly by introducing plant species that have a competitive advantage in the modified habitats.

The first men to modify the habitat were the Australian Aborigines. A lot of nonsense has been written on how the Aborigines have had no effect on the 'natural' environment. The Aborigines have been here for at least 30,000 years and probably much longer. They apparently introduced the dingo and certainly altered the frequency of fires. There is no evidence of their having introduced any species of plant but the possibility of such an introduction must be very real. The Aboriginal population has never been great and their distribution has been more or less limited by the availability of permanent water. It is unlikely that the gathering of food plants has had a great influence on either single species or the vegetation. Once the effort in gathering food plants becomes too great for the return, the species is abandoned as a major food source.

The dingo preys on native mammals and birds and presumably has done so for many thousands of years. Predation alone is unlikely to have caused any of the prey species to become extinct but it may well have changed the relative proportions of the various species making up the herbivore and granivore fauna. It is hard to imagine, though, that the dingo can be allocated anything but a lowly position in any ordering of factors affecting the flora.

Aboriginal man's greatest influence on the flora was by his modification of the environment through fire. It seems unlikely that the Aborigines introduced fire into the Australian environment but there seems little doubt that they altered the frequency and intensity of fire in many plant communities.

It is difficult to assess fully the impact of the Australian Aborigines because their influences have been masked by subsequent

climatic changes. Even if man has been present in Australia for only 30,000 years, there have been at least one comparatively wet and one comparatively dry period in that time. The habitat modifications caused by climatic change are much greater than those likely to have been achieved by Aboriginal man.

What European man saw on his arrival here was a flora and vegetation evolving after a comparatively arid period during the Pleistocene (15,000-18,000 years ago) with Aboriginal man as a component of the environment.

European man has had a greater effect on the Australian flora in 200 years than Aboriginal man has had in more than 30,000 years. At least three plant species seem to have been introduced to precolonised Australia from Central and South America via the early Spanish and Portuguese Pacific trade routes to the Philippines and Indonesia. The three species (*Datura leichhardtii*, *Solanum erianthum* and *Centratherum punctatum*) are native to South America; the last two species are still found in tropical islands on the old trade routes between Australia and South America. The introduction of these three species is not well documented and their actual route and the final steps from Indonesia to the Australian mainland will remain speculative.

After European man established colonies here his modes of action on the flora and the vegetation can be divided into first, indirect and second, direct.

The most significant of the indirect effects has been the introduction of animals that have become naturalised. It is arguable that many of the introduced species actually escaped accidentally but whether by accidental escape or deliberate introduction rabbits, wild goats, water buffalo, camels and wild pigs have had a big effect on the vegetation in some areas. It is a comment on our ignorance that we are not really aware of just how much damage has been done by these animals. Even the European rabbit, which has been widely maligned as the most damaging animal so far introduced (obviously excluding man from the competition!), has probably had its most devastating effects in conjunction with high densities of sheep. Nevertheless, by being independent of surface water for long periods, grazing selectively, grazing very close to the ground and by ringbarking seedlings of some tree species in dry times, rabbits



Above left, a native plant community before man's intervention with brigalow, *Acacia harpophylla*, wilga, *Geijera parviflora*, species of *Lysiphillum*, *Canthium* and numerous species of native grasses including *Chloris*, *Panicum* and *Aristida* species. Typically brigalow communities are replaced by a crop of a single species such as sunflowers, cotton, etc.

Left, our comparatively rare wetlands are on the receiving end of some of the greatest change. This formerly ephemeral swamp has its water level maintained artificially to recharge ground water supplies for agriculture. Adjacent to a large town it receives copious amounts of domestic garbage and fertiliser from the surrounding crop areas. The native palms, *Livistonia decipiens* and paperbarks, *Melaleuca leucadendron*, will probably survive but the smaller native species are being smothered by the introduced water hyacinth, *Eichhornia crassipes* and para grass, *Brachiaria mutica*, in these eutrophic conditions. Photo G. Sainty, other photo Surrey Jacobs.

exerted a more intense and more continuous grazing pressure on many species than previously had been the case. Although these effects have not been well documented, anecdotal information certainly indicates that rabbits changed the proportional species composition of many plant communities.



Feral pigs have affected, and are affecting, other plant communities in ways different from the rabbit. Many of the plant species involved have not been previously subjected to grazing. Pigs root around in wet soil, eating rhizomes and tubers; and tend to congregate around natural wetland areas, a limited resource in much of Australia, thereby concentrating damage on less common plant communities.

Feral goats have survived in areas that were previously inhabited by euros or yellow-footed rock wallabies. Goats apparently have a more catholic diet than either of these species and graze in flocks, concentrating their grazing in plant communities that have previously supported much lower densities of herbivores. Man has aided the goat in this by providing extra watering points for domestic stock.

Water buffaloes in the North have had an effect similar to pigs. Feral camels, horses, donkeys and cattle have all modified the vegetation in certain areas.

The next most significant of the indirect effects man has had on vegetation is the elaborate network of stock watering points established across the country. These watering points have not only allowed the introduction of domestic livestock but have also allowed many native grazing and browsing animals to increase in population size and density. The larger, more mobile species of kangaroos and wallabies have benefited most from the extra water and have, by themselves, subjected many plant communities to more continuous and more intense grazing than had been the case before man's intervention. This increased grazing pressure alone would have been sufficient to slowly alter the vegetation,

A normally dry creek bed that only carried water during floods, has been altered by pumping in water for stock watering. Small barrages have been thrown across in several places creating a chain of more or less permanent waterholes. The sewerage from a nearby mining town also flows into the creek. The net result is the death of the older, larger trees and a community of introduced floating species. These floating species do well in the entrophic water and prevent the growth of submerged fauna. Photo Surrey Jacobs.



but such effects have been swamped by other man-induced changes of much greater magnitude.

The third and most obvious of the indirect influences that man has had is the introduction of exotic species that have been able to compete successfully with native plants in comparatively undisturbed habitats. Fortunately there are not many species in this category but rosy dock *Acetosa vesicaria*, camphor laurel *Cinnamomum camphora* and boneseed *Chrysanthemoides monilifera* are some of the best examples. Rosy dock has successfully established on many of the mountain ranges in arid areas, and has been erroneously included in many slide sets and postcards of native wildflowers. Camphor laurel has become established in many rain-forest gullies of eastern Australia. Boneseed was introduced in an attempt to stabilise areas that had been mined for sand minerals but has moved into undisturbed bushland. Fortunately most introduced species grow on disturbed land and do not move into undisturbed native vegetation.

The more direct methods by which man has altered the flora and vegetation are many and varied. The first stage in the alteration of the vegetation is the primary utilisation of some of the native species. Prime timber species are selectively logged and domestic livestock are used to convert the more palatable plants into marketable protein (meat or wool in Australia). The domestic stock are supplied with water and kept at comparatively high densities with fences. Their dung is different from that of native marsupials and, especially in the case of cattle, not broken down by native dung beetles. Nutrients are removed from the plant communities by the removal of wool and stock. Palatable plant species are often drastically reduced in number while unpalatable species, those adapted to lower nutrient levels, species readily dispersed by animals, colonising species and those capable of tolerating the heavier grazing levels become more common.

The next step in the process of habitat modification is some simple form of plant management. The first attempts are usually aimed at removing plant species that are toxic to stock or, in some other way, hinder the conversion of native vegetation, to marketable protein. Examples are the removal of zamia palms (these are acutally cycads and not related to palms) in Queensland, galvanised burr *Sclerolaena birchii* on sandy areas in western New South Wales and poison pimelea, species

allied to *Pimelia simplex* and *P. trichostachya*, in western Queensland and southern Northern Territory. Methods of removal of these species may be highly selective: for example chipping with hoes; spot spraying with an active herbicide which may kill non-target plants immediately around the target plant; more widespread spraying, for example the so-called defoliants; or cultivation. The less selective the technique, the greater the number of species likely to be affected and the greater the changes to the original vegetation.

The next step is the encouragement of particular species. This encompasses the whole range of agricultural techniques from burning to intensive cultivation, fertilisation and irrigation of a unispecific crop.

Burning alone usually has very little effect. Repeated burnings at high frequencies, annually for example, tends to encourage some grasses and annuals while gradually eliminating perennial woody species and fire-susceptible grasses. Burning, followed by the aerial application of fertiliser and seed of introduced pasture species generally better adapted to higher fertility levels and increased grazing levels, usually results in fire-resistant native woody perennials remaining while the native grasses and herbs gradually decline in importance.

Likewise clearing alone has little long-term effect on many Australian plant communities. Clearing removes all, or all but the very largest, of the woody perennial plants. If nothing else is done the plant community will often quickly regenerate with, after a lapse of many years, only an altered age-class distribution to indicate the brief disruptive period in its history. As with burning it is the follow-up applications of fertiliser, pasture seed and grazing animals which lead to the longer term changes.

Land that is cleared for crops generally receives more careful clearing, stacking and

burning of the existing vegetation, followed by cultivation, once to many times before the addition of fertiliser and seed of the desired species. Some crops are irrigated, further modifying the original environment. Consequently when or if cropland is 'rested' the key phase often omitted in these days of intensive agriculture, the resulting plant community will consist very largely of introduced species whose life cycles are compatible with man's agricultural practices.

Before an area is cleared it may be possible to see one or a few introduced plant species along the road margins. These species have a competitive advantage over many of the native species in this altered habitat. Road margins are frequently graded or scraped free of much of the vegetation. The frequency of this tends to vary with the road usage. In some areas mowing is used instead of, or as well as, grading. Road margins also receive extra water, hard road surfaces absorb very little, if any, water and water runs off to the side, effectively increasing the rainfall for the strip of earth alongside.

In areas that have been extensively cleared and cultivated for cropping, the natural vegetation of the road reserves also tends to have badly suffered, unless these reserves were very broad. Road margins in crop areas have probably had the larger trees removed, to stop branches falling on cars or fences, had varying amounts of fertiliser applied, have been subjected to burning or mowing, received extra water from the road surface, and had various plant species introduced by one means or another. Roadsides are frequently burnt to prevent fires spreading into crops but may be burnt again if the crop stubble is burnt. Fortunately this latter practice is declining these days but in areas where it is still practised roadsides may be burnt twice a year. Consequently roadsides often have varying mixtures of weeds, pasture plants and native species all struggling for space.

Classic symptoms of progressive urbanisation. In this case it is a mangrove community being destroyed. Earth filling based on surveyor's lines rather than drainage patterns has altered the tidal flushing, killing the young mangroves that had re-established after the construction of the high voltage power lines. Unfortunately the damage is continuing by the practice of dumping domestic and industrial garbage throughout the area. Photo Surrey Jacobs.



A notable exception to this roadside syndrome can be seen along some of the less developed roads of the Western Australian wheat belt where road maintenance has not particularly upset the plants in comparatively broad road reserves. The absence of fences or car-damaging trees and the presence of fire tolerant heath has resulted in roadside plant communities remarkably similar to the original plant communities. An unfortunate corollary to this particular pattern of clearing is that in many areas the only native vegetation left is along the road reserves and many native species are now found nowhere else.

The clearing of vegetation and alteration of the environment is carried to extremes in urban and suburban developments. Such developments reduce the amount of rainfall reaching the ground by intercepting the rain, and alter drainage patterns by either running the water onto other areas or removing it completely from the site. Concentrated use of small areas of land and increases in fertility as a result of domestic gardening gradually alter any remaining areas of native plants, resulting in a gradual decline in the number of native species, even in areas intended for their preservation.

Some aspects of the environment are not compatible with suburban development. The best example in Australia is the occurrence of wildfires. Much of our vegetation is adapted to intense fires every ten or twenty years. Our houses and finance systems are not adapted to such natural phenomena, so suburban developments in fire-prone areas are surrounded by a zone of managed natural vegetation. The management varies from an extensive system of fire-breaks and access roads, 'fire trails', to a management plan of 'controlled burning'. Controlled burning increases the frequency but decreases the intensity of the fires. Presumably such a system will result in gradual long-term changes in some vegetation types.

Coupled with man's undoubted abilities to alter the original environment is his propensity to introduce and spread other plant species that are attuned to the new environment and have a competitive advantage over the native species. Apart from species that are agriculturally important, for example *Paspalum dilatatum*, kikuyu *Pennisetum clandestinum*, and white clover *Trifolium repens*, there are species that were originally introduced as ornamental subjects, for example, privet *Ligustrum* spp., most of the

oxalis species *Oxalis* spp., camphor laurel *Cinnamomum camphora* and wandering jew *Tradescantia albiflora*.

Most weeds, however, were introduced and have spread because of characteristics that have allowed them to be dispersed unintentionally by man's everyday activities. The more economically important weeds are adapted to grow in crops and are spread by crop harvesting and handling techniques. These weeds include black oats *Avena fatua*, Mexican poppy *Argemone ochroleuca* and saffron thistle *Carthamus lanatus*. Other species spread on clothes (the discarding of the trouser cuff fashion slowed down many species), vehicles or sacking, for example stock feed, seed wheat, wool bales. Livestock with fruits or seeds adhering to their hair, fur, wool or feathers, or with seeds passing intact through their digestive tracts, may be moved hundreds of kilometres with the aid of mechanised transport.

Some of the more unfortunate examples of the spread of weeds are where the plants are intentionally moved around the country as ornamental species but, once the novelty has worn off, are discarded into habitats where they can cause immense changes in the natural systems and often cause problems in agricultural areas. The best examples here are water weeds, possibly because it is easier to trace their origin in a localised and well-defined habitat. *Salvinia* *Salvinia molesta* was introduced from a home pond into Lake Moondarra near Mt Isa, and by similar means into small creeks throughout New South Wales and Queensland; water lettuce *Pistia stratiotes* was introduced into some river systems in eastern Queensland; water hyacinth *Eichhornia crassipes* is common throughout Australia and invariably is spread between water catchments from home ponds. All of these floating water plants prevent light from reaching the native submerged vegetation, thereby depleting the dissolved oxygen in the water, and killing off native flora and fauna.

Although man has altered large areas of Australia, some have been saved, at least temporarily, and included in national parks. Some parts of the continent have felt many of man's changes, others very few. Most areas have probably received a unique combination of indirect and direct interference but often one influence, or very few, of these is of such magnitude that the subtleties which could be expected from such combinations have been lost.

If man was suddenly removed from Australia now and, at some time in the future, the flora and vegetation were analysed in an attempt to interpret their history, it would be interesting to speculate on the magnitude of the changes we have initiated. Would they be comparable to the influence of continental drift or to the effects of an Ice Age? The one disturbing thought here is the time scale. Continental drift has been important on the scale of millions of years, Ice Ages over at least hundreds of thousands. We have done it all in 200 years.

FURTHER READING

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Three main phases in the sequence of separation and drift of continents were of importance in determining the origins and evolution of the flowering plants in Australia. This movement helps to explain the similarities of plant families in continents on opposite sides of the globe and perhaps the perplexing exceptions of those families endemic to Australia which seem to have been . . .

by Laurie Haegi



Cypanthera ablicans is a member of the distinctive Australian tribe Anthercerideae of the family Solanaceae. The family is otherwise chiefly developed in South America and its occurrence on both continents is explained by the events of continental drift. Photo: Laurie Haegi.

Two apparently conflicting traits exhibited by the plants of Australia—their distinctiveness and yet their relationship with floras of different lands—have fascinated botanists for more than a century. Laurie Haegi, a botanist at the National Herbarium of New South Wales, describes how the recent acceptance of continental drift theory has satisfactorily reconciled these observations and provided new ideas on the origins of the Australian flora.

Australian *Eucalyptus* forests and shrublands 'mallee' and heathlands with their well-known grevilleas, banksias and waratahs are so characteristic that it would be easy to think that Australia's flora had evolved in total isolation. Given the vast expanses of ocean that surround the Australian continent on the eastern, southern and western sides and the lack of any close connection with a major land mass in the north, this might not be an unreasonable conclusion. But such a conclusion would be wrong.

Even the most cursory inspection of the floras of other continents reveals that, although few of our species occur elsewhere, many plant families, and even those which contain the very plants that are distinctive in our flora, are found widely on other land masses. Thus, the family Myrtaceae, of which familiar genera such as *Eucalyptus*, *Melaleuca*, *Callistemon* and *Leptospermum* are members, is also represented (by different genera) in South and Central America, on islands of the Pacific, in southern and eastern Asia, in South Africa and even in the Mediterranean region. Similarly, the close relatives of *Banksia*, *Telopea* (Waratah) and *Grevillea* (all family Proteaceae) are found in South Africa, eastern Asia, on Pacific islands and in South and Central America. In fact, as the Australian flora is compared more closely with the floras of other continents, it becomes clear that very few families are restricted to it and that a surprising number of genera found in Australia are represented by different species elsewhere.

Today there is little doubt that the land plants had a single, common origin. Almost all of the major land-plant groups (the liverworts and mosses, clubmosses, ferns, gymnosperms: conifers and relatives, and flowering plants) are found in Australia, just as they are found on most continents and subcontinents of the world. How did these groups of plants, which are dependent on land for survival, come to be distributed so evenly across these far-flung land masses?

Traditional explanations have involved long distance dispersal and land-bridge theories. Long distance dispersal is the chance transport of the seeds or spores of plants, especially over expanses of ocean, to distant lands. Various agents, notably winds, ocean currents and migratory birds effect the dispersal. While this mechanism has undoubtedly played a role in the wide distribution of many plants and plant groups, the limitations imposed by the lack of appropriate wind directions, sea currents and bird migration patterns,

CAUGHT IN THE DRIFT

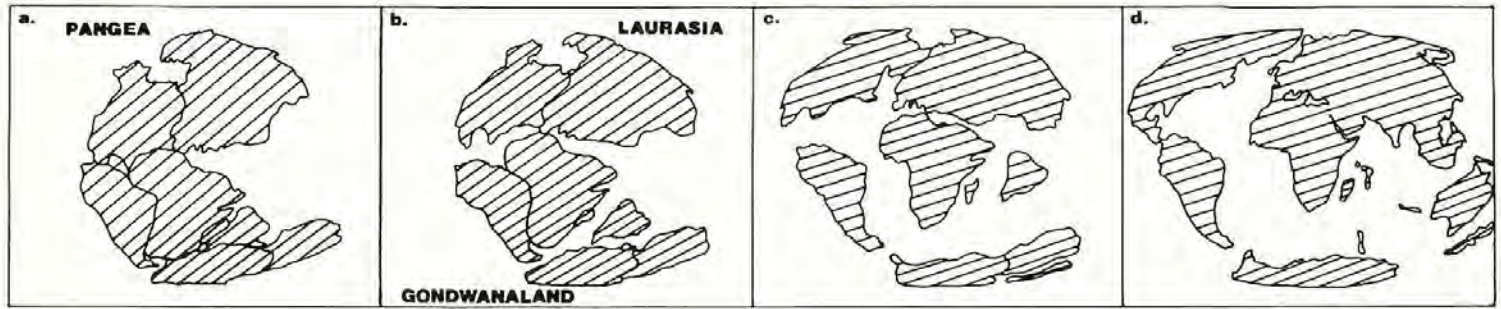
the limited viability of disseminules in seawater, the likelihood of unfavourable environments at the point of deposition and the restrictions imposed by large- and heavy-seeded plants, all dismiss this as a sole explanation. The once popular notion that in ancient times narrow bridges of land stretching across the oceans of the world enabled the interchange or migration of plants and animals among the continents is now seen to be supported only in very few cases.

In 1912 the German scientist Alfred Wegener proposed a radical theory on the history of the land surfaces of the earth. His theory was that, far in the geological past, only one large land mass existed. He named this Pangaea, meaning 'all lands'. This land mass had successively broken up, with the pieces moving apart, eventually resulting in the arrangement of continents around the world as we know it today. With this the theory of continental drift was born.

This theory provided by far the best explanation of many of the disjunct distributions of plant groups around the world and was supported by various kinds of geological evidence. The continents clearly fitted together reasonably well, and when the slightly different outlines of their submerged continental shelves were plotted, the matching was dramatic. Added to this, rock types were found to match on corresponding parts of different continents and identical fossils found in different parts of the world.

Despite this strong circumstantial evidence for the idea of continental drift it was largely rejected by geological scientists for over half a century because of the lack of any feasible explanation for the moving about of enormous continental land masses. Biologists were divided by the issue, some attracted by the eminently satisfactory explanation the theory provided for their biogeographical observations and others unconvinced, clinging to refined versions of more acceptable early ideas, especially the land-bridge theory. To some, the evidence suggested that although the idea of drifting continents was acceptable it must have occurred far too early for it to have any influence on the distributions of most groups of plants and animals.

Then, during the 1960s, with the help of technology not previously available, a revolution began in the earth sciences, culminating at the end of that decade in the emergence of the theory of plate tectonics. Backed by virtually indisputable geological, geophysical and



Phases in the break-up and drift of the continent

- a) 200 million years ago there existed a single supercontinent, Pangaea.
- b) By 180 million years ago these had broken into two major land masses the northern 'Laurasia' and southern Gondwanaland.
- c) At 65 million years ago Africa and Greater India had separated and become distant from the other southern continents, leaving these (South America, Antarctica and Australia) as an elongated almost continuous land mass.
- d) By 15 million years ago Australia was distant from Antarctica and had approached the south-east Asian region.

palaeomagnetic evidence, this theory rapidly became accepted. Simultaneously, it provided a better understanding of the history of the earth's crust and a credible mechanism for the displacement of continents.

Rather than being fixed and continuous, the earth's crust is composed of several plates that move relative to one another. Through a process known as sea-floor spreading, these plates move apart and grow laterally with the addition of lavas forced up by powerful convective currents in the magma beneath the crust. On their opposite sides the plates are thrust deep into the earth's mantle, again becoming part of the magma. In this way, the lighter, buoyant continents are gradually rafted to new positions, on a time scale of tens and even hundreds of millions of years. This drifting is still occurring and has been measured at rates of up to 10 cm per year. The study of palaeomagnetism utilises the fact that, as lava solidifies, certain minerals it contains become fixed in alignment with the earth's magnetic field. Because the polarity of the earth's field changes periodically the age of different parts of the sea-floor can be readily determined and past configurations of the continents reconstructed.

With the support of these theories, the existence of the supercontinent of Pangaea until about 200 million years ago is generally accepted. At that time, it began to break into two smaller supercontinents, Laurasia and Gondwanaland, which in turn fragmented into the continents largely as we know them today. Beginning about 125 million years ago, when the two supercontinents were for the most part separated by an expanse of sea, Gondwanaland began to break up with the rotation of Africa-Madagascar away from South America and the rift of Greater India (including much of present-day India, Nepal, Iran, Thailand and possibly part of China) from

Africa-Madagascar and Australasia-Antarctica. Around 80 million years ago, New Zealand and New Caledonia separated from Australia leaving it connected to East Antarctica. In close proximity was West Antarctica which virtually abutted onto the southern tip of South America. This essentially continuous elongated land mass remained intact for another 30 million years until about 49 million years ago when Australia began rifting from Antarctica; by 38 million years ago overland connections were severed. At 15 million years ago the Australian and Asian plates collided eventually forming the geologically composite island of New Guinea. By this time, Greater India, having begun its northward movement approximately 70 million years ago, had undergone a violent collision with Eurasia at 40 million years ago, leading to the origins of the world's largest mountain range, the Himalayas.

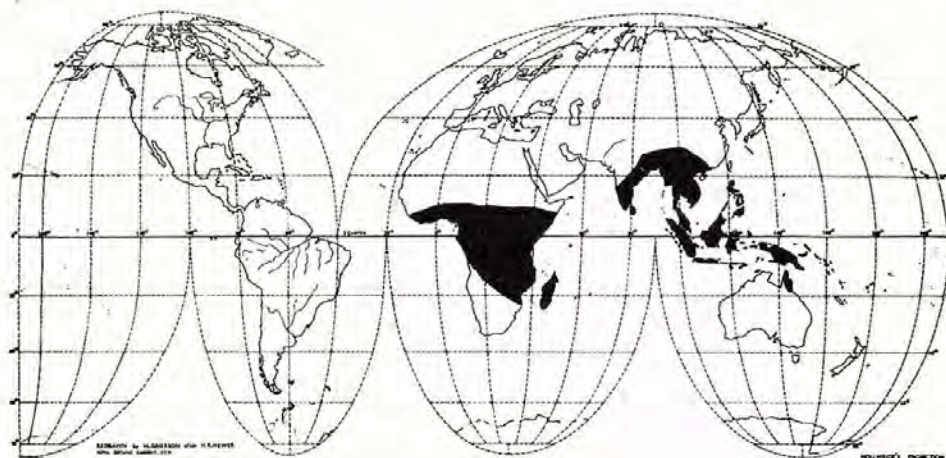
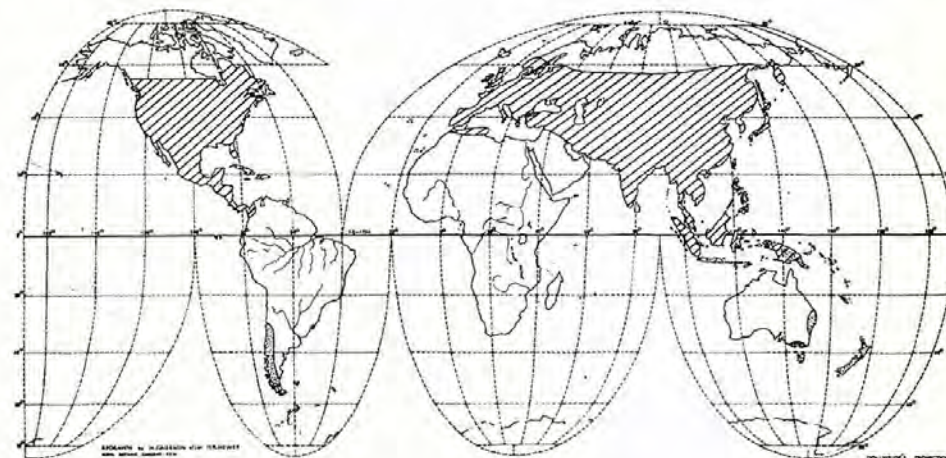
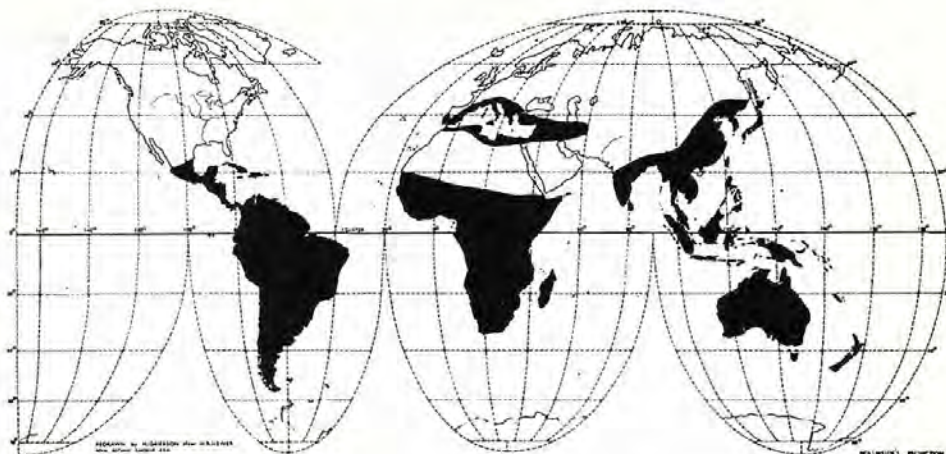
Against a geologically-based backdrop of the fragments of supercontinents drifting apart and later re-uniting in different configurations, an improved picture of the origins of the Australian flora can be developed. Some aid to interpretation is provided by studies of fossils, especially fossil pollen. Because of their tough outer wall, pollen grains, which frequently are characteristic for particular groups of plants, were often preserved in sediments when other softer, less resistant materials rapidly decomposed. Radiocarbon dating techniques allow quite accurate ages to be assigned to many of these deposits, giving excellent indications of past distributions of the ancestors of various modern lineages of plants and of the assemblages of plants making up the vegetation at those times.

At the time of breakup of Pangaea 200-180 million years ago, the vegetation consisted primarily of gymnosperms (conifers and cycads), ferns, and the long-extinct seed-ferns. As might be expected, these groups are represented by their modern counterparts, though in some cases only by fossils, on all or most continents today. The subsequent events which isolated the various parts of Pangaea are responsible for the frequent occurrence of distantly related lines within these groups on different continents, and in particular on the land masses of the northern as compared with those of the southern hemisphere today. The genus *Pinus*, and indeed the family Pinaceae, species of which made up a considerable part of the extensive coniferous forests of Eurasia and North America, is entirely absent from Australia, where, for example, the very different bunya pines *Araucaria* and their relatives are found,

though on a scale which is minuscule by comparison. Although similar patterns of relationships occur to some extent in the ferns, the easy dispersal of their spores by wind in part accounts for their wide present-day distribution.

Today, the most conspicuous, abundant, diverse and widespread components of terrestrial vegetation are flowering plants, or angiosperms. One of the greatest mysteries facing plant scientists is the sudden rise to dominance of a wide range of angiosperms almost simultaneously on all land masses of the earth. The earliest fossils assignable with certainty to the angiosperms are pollen grains dated at 127 million years ago, found in Africa, South America, Eurasia and North America. These observations suggest a very rapid evolution and dispersal amongst the first flowering plants and are critical in reconstructing the origins of the floras of the different continents, since it was around this time that the continents began separating from one another and drifting apart, greatly restricting migration. Also of key importance in this regard is the place of origin of the flowering plants.

Because many primitive families of flowering plants occur today in South East Asia it has been suggested that the angiosperms originated there. Australia also has been proposed as a centre of origin, because of a rich representation of primitive flowering plants in the rainforests of northeastern Queensland, sometimes including the only living representatives of such groups. While these views cannot be entirely discounted, there is more evidence at present for another hypothesis: that the flowering plants had their origin in West Gondwanaland, the area formed by the combined continents of South America and South Africa. This notion is supported by reconstructions of contemporary climatic conditions in that region, indicating extensive aridity in the interior of the vast land mass, surrounded by moist forests. Climatically transitional areas have been especially important as centres for plant evolution. Relatively free migration of these early flowering plants to Antarctica, Australasia and India eastwards and to North America and Eurasia in the north would have been possible from West Gondwanaland. Poor representation of primitive flowering plants in Africa and South America today can be explained by their elimination as a result of catastrophic climatic events which occurred in these regions over subsequent periods of time. According to this view, some of these early groups were able to



survive in climatically favourable refuges in suitable parts of the Australian continent and eastern Asia, migrating only in relatively modern times to South East Asia.

Three main phases in the sequence of separation and drift of continents were of importance in determining the origins and evolution of the flowering plants in Australia.

As already stated, at the time when the flowering plants first appeared, migration across Gondwanaland was relatively unrestricted and intermittent connections of Africa with Laurasia also allowed dispersal northward. During this phase the initial diversification within the flowering plants was taking place, giving rise to the ancestors of what are now the major groups: orders and suborders (aggregations of families). Hence both major groups within the flowering plants, the monocotyledons and dicotyledons, are present in Australia as on all vegetated continents. Several orders, especially those containing primitive families such as the Winteraceae, represented in Australia by the genera *Tasmannia* and *Bubbia*, though generally uncommon, are globally widespread. The spread and subsequent breakup of the ranges of these early-evolved orders has provided the Australian flora with a significant proportion of the small number of endemic or near-endemic families found here, e.g. Austrobaileyaceae, Idiospermaceae, Eupomatiaceae. The ancestors of families such as Casuarinaceae: she-oaks; Araliaceae; Epacridaceae: heaths; Myrtaceae; Cunoniaceae, e.g. *Callicoma*, Blackwattle; Santalaceae: sandalwoods; Dilleniaceae: guinea flowers; Proteaceae; Thymeleaceae: rice flowers; Rutaceae: *Boronia*, *Eriostemon*; Xanthorrhoeaceae: grass-trees; and Restionaceae, would have reached Australia during this first phase, when a warm-temperate to subtropical route was available.

As Greater India and Africa-Madagascar rifted from the rest of Gondwanaland, migration amongst some parts of the southern land mass and interchange with Laurasia became increasingly interrupted. During this time, 125-70 million years ago, most of the families and some of the genera of flowering plants were becoming differentiated. With considerable opportunity for dispersal some of these became widely distributed probably from West Gondwanaland across Africa-Madagascar, India and to Australasia and Antarctica. Such a route is understood to account for the presence of the family Fagaceae (oaks, beeches) in Australia, where it is represented

World distribution of family Myrtaceae (top), showing the concentration on southern-hemisphere land masses.

World distribution of the primarily northern hemisphere beech family, Fagaceae (centre). Almost the entire southern-hemisphere distribution (dotted areas) is accounted for by the ancient genus *Nothofagus*.

World distribution of the Banana family, Musaceae (above). This tropical family reached Australia in relatively recent times from south-east Asia after the collision of the Australian continent with this region 15 million years ago.



Australian rainforests harbour representatives of ancient lines of plants which arrived here very early in the history of continental drift. One such plant is *Eupomatia bennettii* of the Eupomatiaceae, one of the few families endemic to Australia. Photo A. N. Rodd.

by the Antarctic Beech genus, *Nothofagus*. The occurrence of this southern outlier of an otherwise northern hemisphere family had long puzzled biogeographers; its extensive occurrence in the fossil record indicates that this ancient genus, now found only in small pockets in New Zealand, New Guinea, eastern Australia, Tasmania and South America, once formed extensive forests over much of the supercontinent of Gondwanaland. While migration, particularly north-south, was facilitated by climates more equable than those of the present day, factors other than the lack of direct overland connections must have been operating to account for the restriction of some groups to the southern land masses.

The end of the first phase is marked by the separation of New Zealand from eastern Australia 80 million years ago (this accounting for the surprising paucity of close relationships between the Australian and New Zealand floras) and the beginning of the rapid northward movement of Greater India towards the Eurasian land mass at 70 million years ago. The latter event rapidly diminished the chances of dispersal between Africa and the remaining southern continents and consequently between the southern and the northern land masses.

For the following 20 million years or so, the relatively elongated Gondwanaland remnant, consisting of South America, West and East Antarctica and Australia, was isolated on the whole by increasingly large tracts of ocean from the remainder of the world's terrestrial environments. Those groups present on the southern continents were to undergo evolution in isolation, producing a distinctive element in the flora of the world. Relatively free migration within the Gondwanaland remnant was possible with a broad overland connection between Australia and East Antarctica while the connection of the latter with South America was via the narrow archipelago of West Antarctica. At this time, these continents

were all in very high latitudes, with a cool-temperate climate prevailing. Northern Australia was somewhere near the current latitude of Melbourne. Although the extreme southern parts of Antarctica were becoming glaciated, vast areas of the southern land mass were vegetated with cool-temperate *Nothofagus* forest.

During this period of isolation many southern groups became diversified and today form a distinct element in the Australian flora. This sequence of events is reflected in closer relationships with the South American than the South African flora. One group particularly well studied in this regard is the family Proteaceae, one of the classically southern families. Of the five subfamilies in Proteaceae, all are present in Australia. While two are found in South Africa and only one in South America, the link with South Africa goes only to the next lowest (tribal) level, but in the case of South America, genera, *Oreocallis*, *Orites*, *Lomatia*, are shared with Australia. The main South African element, the tribe Proteaceae, is restricted to that continent.

The family Myrtaceae, so prominent in the Australian flora, not only with the major and frequently conspicuous genus *Eucalyptus* but also with many other sizeable genera representing both subfamilies, shows a major development during this period of isolation. Myrtaceae are very poorly represented in South Africa with only four genera, contrasting the 95 Australasian and 47 South and Central American genera. Many other families or major groups within families exhibit similar trends. Over a period of 20 million years, several waves of migration and complex interactions involving climatic, vegetational and probably topographic changes would have resulted in plant groups showing intercontinental relationships at more than one level. In the Solanaceae, to which the tomato, potato, capsicum and tobacco all belong, a family of apparently South American origin, different times of origin for the Australian represen-

tatives are apparent. Early in the evolution of the family, the ancestors of the distinct tribe *Anthocercideae* would have migrated from South America to Australia via Antarctica. The distinctiveness of the *Anthocercideae* and distribution of characteristics within it, together with its modern occurrence only in warmer regions, supports the notion that it had cool-temperate ancestral lines which are now extinct. The ancestors of the genera *Solanum*, a large, chiefly South American but widespread genus of over 1,000 species, and *Nicotiana*, the tobacco genus, also shared chiefly with South America, would have reached Australia in a much later wave of migration. Their subsequent isolation from South America, which has persisted to the present day, is reflected in the evolution of many species in groupings peculiar to the Australian region. Other families or orders which are well developed in both northern and southern hemispheres have distinctive Australian elements. Such groups are the Chloanthaceae, close to the Verbenaceae, Verbena family, and the subfamily Prostantheroideae (*Prostanthera*, *Westringia*) of Lamiaceae, the mint family, which had probably reached Australia by this time.

As the Australian continent began rifting from East Antarctica 49 million years ago, another phase, which was to have a profound influence in shaping the Australian flora, began. By 40 million years ago the initial stages of separation were complete and Australia began moving northwards, while South America continued converging on North America. The effects of these continental movements were far-reaching. Not only was Australia to be largely isolated for a period of 25 million years but it was also to pass further and further into lower, and consequently warmer and drier latitudes, resulting in the gradual but widespread destruction of the cool-temperate vegetation it carried. This in turn was to provide ideal conditions for rapid evolution through adaptive radiation in many groups. At the same time, the movement of these land masses away from their southerly

The family Proteaceae is one of the best examples of a group which evolved and dispersed on the fragments of the southern land mass Gondwanaland. A less well-known representative of the family is *Isopogon anemonifolius*, drumsticks. Photo J. M. Baldwin.



positions resulted in the development of circum-polar winds, leading to drastic cooling in that region, extensive glaciation, and the consequent decimation of the cool-temperate forests of Antarctica.

It is during this period of isolation and entry into warmer and drier climatic zones that much of the modern Australian flora evolved. Large-scale extinction was balanced by rapid evolution of species adapting to the drier conditions. Towards the end of this period the components of the characteristic Australian sclerophyll forest and shrubland vegetation underwent extensive expansion on the poorer soils. This is true of families such as Proteaceae, Myrtaceae, Epacridaceae and Fabaceae, which predominate in the sclerophyllous vegetation today. Other families underwent diversification especially in drier areas of the interior where soil fertility may not have been such a limiting factor. Many species of families like the Chenopodiaceae, which provide the saltbushes and bluebushes of the southern arid shrublands today, the Mimosaceae, to which the largest and possibly most ubiquitous Australian genus, *Acacia*, belongs, the Myoporaceae, including the large genus of Emu Bushes, *Eremophila* and the Asteraceae or daisy family, widespread in arid and semi-arid areas, diversified extensively in these regions. At the same time, the wetter coastal districts of eastern Australia provided refuges, which today still harbour small numbers of descendants of components of the earlier flora. Many climatic fluctuations have since resulted in further speciation and extinctions but the major phase establishing many of the dominant groups over much of the continent preceded these.

Finally, 15 million years ago, the Australian plate collided with the Asian plate, opening pathways of interchange with the northern flora for the first time in more than 50 million years. The cool-temperate relictual groups found in the higher altitudes of north-east

Australian tropics were able to spread to similar areas in New Guinea and South East Asia, e.g. *Nothofagus*, Winteraceae, Eupomatiaceae). Later, other more characteristic Australian groups such as *Eucalyptus*, *Grevillea* and *Banksia* were to extend their ranges of occurrence into tropical regions to the north.

Conversely an influx of species of northern origin from groups which had developed in the tropical South East Asian region produced a further distinct element primarily in the tropical Australian flora. The Australian representatives of Verbenaceae, e.g. *Clerodendron*, *Callicarpa*; Meliaceae, e.g. *Melia azederach*, White Cedar; Melastomataceae; Nepenthaceae: pitcher plants; Musaceae: bananas; and Zingiberaceae: ginger, have such an origin.

Prior to the firm establishment of plate tectonic theory and the acceptance of the occurrence of continental drift, attempts had been made to recognise the major elements in the Australian flora and to discover their origins. Many of the conclusions reached at that time have now been shown to be in error. The improved knowledge of the history of the earth's land surfaces has without doubt led to enlightenment on some aspects of the origins of the Australian flora. In particular, it is possible to recognise groups belonging to an ancient southern element on the one hand and northern groups with a much more recent Australian origin, on the other. But further refinement of this understanding perhaps for the greater part of the flora, often rests on rather slim evidence.

Before further headway can be made a great deal of work is needed to increase the knowledge of relationships within and among the families of terrestrial, especially flowering, plants. Advances in the earth sciences have led to and will undoubtedly continue to lead to refinements in the geological models of continental drift. As the fossil record grows an

improved knowledge of past distributions, of the time of the appearance of various plant groups, and perhaps, the effects of plant-animal interactions, will emerge. But a better understanding is also needed of the other factors such as climatic gradients and changes and regional or even large-scale topographical alterations, with associated localised climatic changes, which in many cases must have had an equally important impact on the evolution and dispersal of plant groups. Even now the interpretation of many observed disjunctions in ranges of major groups depends on such factors. The effects of repeated medium and long distance dispersal over these long periods of time can be indistinguishable from the results of continental drift. Despite the major contribution to knowledge of the origins and evolution of different plant groups, and of the Australian flora in turn, made in the light of continental drift, its most valuable effect may have been in raising more problems than it has solved. At the same time, it has provided more relevant questions to be asked in trying to solve these problems.

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LEAVE IT TO THE BIRDS AND BEES

Pollination is a complex process which involves the interaction of a vast number of pollinating agents, including birds, mammals and insects, as well as wind and water, to Australia's many different plants. With interest in pollination biology growing rapidly in Australia and the fact that it touches on so many other areas of biology, especially ecology, its future is promising. Graham Pyke is presently attached to the Australian Museum on a government research grant and is studying the ecology of honeyeaters and their methods of foraging food.

by Graham H. Pyke



Above, the slender flowers of *Pimelea linearifolia* are well suited to pollination by this moth, *Pollanisus* sp., which obtains nectar from the bases of the flowers with its relatively long proboscis. Photo J. Armstrong.

Left, the eastern pygmy possum is a small, nocturnal marsupial which is widespread in south-eastern Australia where *Banksias* are common and there is a relatively dense understorey of shrubs and small trees. Nectar and pollen are major components of this possum's diet. In the process of collecting these foods it acts as a pollinator, transferring pollen on its fur from one flower to another. The *Banksia* shown here is *Banksia coccinea*. Photo T. Newbery.

Modern pollination biology which is attracting more and more interest encompasses a rather wide variety of interrelated subjects. To fully evaluate pollination biology one must consider the pollination process itself, which involves the transfer of pollen between flowers. Also to be considered are the events occurring after the pollen reaches the flower and the entire path from pollination through seed set and seed dispersal to germination and subsequent growth of a new plant. The agents that bring about the pollen transfer are also important as many aspects of the behaviour and ecology of some of these agents are affected by the availability of pollen and nectar, the floral resources that attract animal pollinators.

Pollination biology began with observations by people such as Aristotle who in about 350BC observed an association between bees and flowers.

The most important parts of flowers fall into two parts, the pollen, carrying the male genetic material, and the ovules, carrying the female genetic material. Fertilisation occurs when these two kinds of genetic material meet and unite. Usually this involves pollen from one flower being transferred to the appropriate part of another flower allowing pollination.

Nectar, another important component of many flowers, is essentially a sugar and water solution. There are many kinds of sugars, however, and several of these are always found in nectar. Nectar sugar consists mostly of sucrose, the sugar many of us put in our tea and coffee, plus fructose and glucose and small amounts of other sugars such as maltose and raffinose. Besides sugar, nectar contains very small amounts of a quite vast array of different sorts of chemical compounds. These include amino acids, proteins, lipids, mineral salts—even alkaloids, a kind of organic poison.

Petals and occasionally sepals are the most conspicuous parts of many flowers. They, along with the nectar, pollen and sometimes odour, serve to attract potential animal pollinators to the flowers.

A truly remarkable diversity of agents act as flower pollinators. Wind and water are two that form a non-biotic category. The well-known she-oaks, *Casuarina* spp., are wind pollinated, as are many of the showy wattles, *Acacia* spp. Water-pollination is very rare. Biotic or animal pollinators include various birds, mammals and insects. Insect pollinators

include not only the familiar bees but also wasps, butterflies, moths, flies, beetles and, on rare occasions, even ants and thrips. These different sorts of animals visit flowers to obtain pollen or nectar, and in so doing, pick up pollen on their bodies and subsequently transfer this pollen to other flowers. In this way these animals bring about pollination.

The principal bird pollinators in Australia are the honeyeaters, a family of nectar-feeding birds, *Meliphagidae*, essentially restricted to our continent and to nearby New Guinea. These birds pollinate many of our most beautiful flowers, including waratahs, *Telopea* spp., bottlebrushes, *Callistemon* spp., kangaroo paws, *Anigozanthos* spp., and some of the gum trees, *Eucalyptus* spp., and spider flowers, *Grevillea* spp. There are about 70 species of honeyeaters in Australia and they are found in abundance throughout the country, both in the bush and in suburban gardens. In fact, it is possible through judicious choice of garden plants to encourage these birds to occupy suburban environments. The spectacularly coloured lorikeets or brush-tongued parrots may also act as pollinators of some of our plants.

Bats are the best known mammal pollinators. Some bats have diets that include pollen and nectar. These bats fly between flowers at night carrying pollen on their fur. In Australia bat-pollination is probably restricted to tropical regions and few examples have so far been reported. Unique to Australia is another form of mammal pollination—that carried out by two kinds of small marsupial, the honey possum, *Tarsipes spencerae*, and four species of pygmy possums, *Cercartetus* spp. These marsupials have recently been found to be important pollinators of many Australian plants, especially some of the banksias. Non-flying mammal pollination, as this kind of pollination is usually called, also occurs in Africa. Interestingly, the African plants involved are fairly closely related to the banksias, being in the same family Proteaceae.

Most Australian plants are pollinated by insects, especially bees. There are about 2000 species of bees in Australia, every one of which has a pollen and nectar diet. They pollinate such plants as tea trees, *Leptospermum* spp., paper barks, *Melaleuca* spp., some wattles, many of the native peas such as *Pultenaea*, *Hovea*, cassias, *Cassia* spp.) and probably most eucalypts. Much less prevalent are plants pollinated by other sorts of insects.

Many flies have specialised diets of pollen and nectar and act as pollinators of the plants they visit. The yellow blossom of *Hibbertia scandens* is a source of pollen to these syrphid flies, *Melangyna viridiceps*. Photo J. Armstrong.

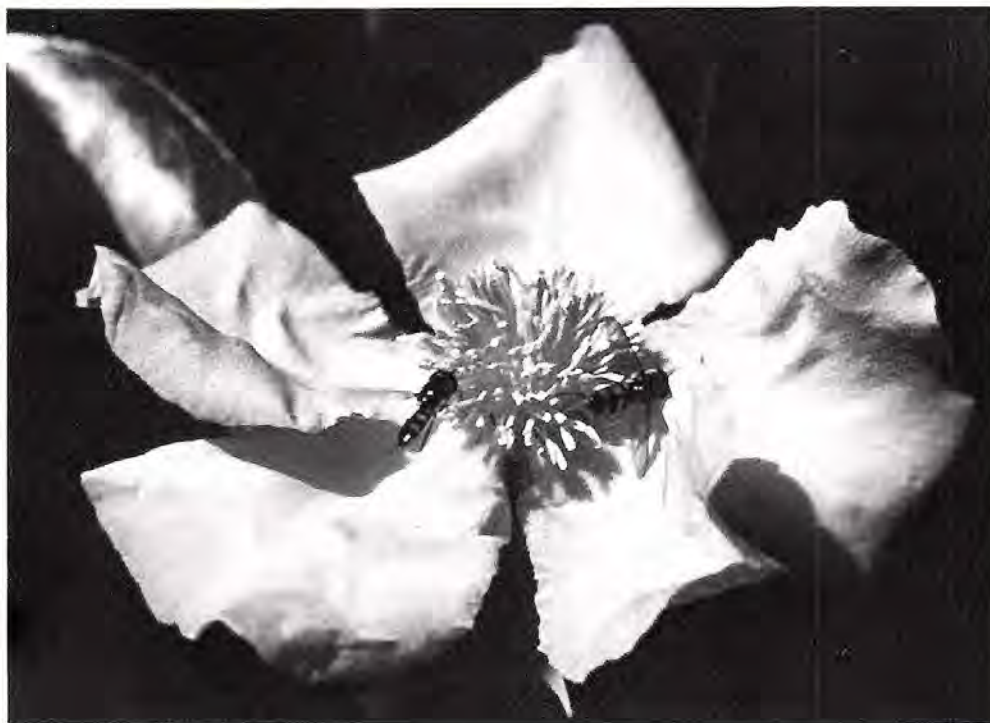
Pollination is obviously advantageous to the plants involved providing sexual reproduction and giving the animals food in the form of nectar and/or pollen. Nectar provides an important, and, in some cases, the entire source of energy to the animals that collect it. Pollen, on the other hand, provides the protein upon which the growth and reproduction of animals depend. Nectar and pollen are used as food by all of the kinds of animals.

Once the nature of the pollination process was understood, pollination biologists began to notice various patterns in terms of the associations between plants and their pollinators. These patterns, or 'syndromes' as they are usually called, consist of relationships between plant traits such as flower colour, odour and shape and the type of pollinator involved. In fact, it is often possible to tell just by examining the flowers on a plant what pollinates the plant. This is not always reliable, however, as there are exceptions to all the patterns.

The following patterns in terms of flower colour have been discovered. Plants pollinated by nocturnal animals such as bats and moths tend to have flowers that are very pale coloured (for example, white or cream). By comparison, day-pollinated flowers show a variety of colours, especially red, yellow and blue. Amongst these day-pollinated plants, those pollinated by birds tend to have red flowers while those pollinated by bees tend to have flowers that are blue or yellow.

Whether or not flowers have odour appears to depend on whether they are pollinated during the day or at night. Night-pollinated flowers tend to produce strong scents. The introduced honeysuckle, *Lonicera japonica*, provides a good example. Many a garden becomes filled with the sweet aroma from these flowers when they are in bloom. Day-pollinated flowers on the other hand, tend to be unscented.

There also tends to be a close match between flower shape and the shape of the pollinators heads or mouthparts. Bat-pollinated flowers, for example, tend to be large and funnel-shaped. Bird-pollinated plants tend to have tubular flowers of similar length and bore to the lengths and thicknesses of the birds' beaks. Moth-pollinated plants typically have quite long, thin tubular flowers, which correspond well to the long, narrow proboscises



of the moths. Finally, bee-pollinated flowers tend to be open or short-tubular.

There may be associations between pollinator type and other floral traits besides flower colour, odour and shape and recently pollination biologists have begun to investigate such possibilities. One particularly fascinating pattern that has begun to emerge from these studies involves the concentration of amino acids in nectar. Plants with relatively high concentrations of amino acids in their nectar tend to be pollinated by animals which do not at the time have an abundant alternative source of amino acids. Plants, for example, that are pollinated by birds, which can easily obtain amino acids from insects, tend to have relatively low amino acid concentrations in their nectar. At the other end of the spectrum are plants pollinated by butterflies and moths, which, as adults, usually have no source of amino acids in addition to nectar. Plants pollinated by these animals tend to have nectar with relatively high amino acid concentration. Even in these cases, however, the level of amino acids in the nectar is far lower than that of sugars.

In virtually all of these associations between plants and their pollinators it can be seen that the relationship is a 'mutual' one. Both the plants and the animals gain something. The plants obtain sexual reproduction through animal-mediated pollen transfer and the animals gain nectar and/or pollen.

Pollination biology also extends to studies of the distribution and abundance of the animals involved. In western North America, for example, there is a regular seasonal migration of hummingbirds that coincides with the availabilities of their nectar sources in different localities. In the spring these birds migrate northwards through low elevation parts of California. During this time these areas offer an abundance of flowers that precedes a rela-

tively dry flowerless summer. In the summer the birds are found in the mountains throughout western North America, where they take advantage of the brief respite from cold, snowy conditions and the dense meadows of summer flowers. During autumn the birds move southwards down the chain of mountains to their wintering grounds in Mexico and points further south. Only in these southern areas can the birds find flowers in the winter.

In Australia the situation seems somewhat different. With few exceptions Australian honeyeaters show little evidence of regular long distance migrations. This could easily be a consequence of our relatively benign climate that permits flowers to bloom in most areas at any time of the year. There are, however, striking variations in flower abundance from one place and time to another. Consequently it is not surprising that our honeyeaters seem to move about and to aggregate in areas of relatively high floral abundance. Sound management of honeyeaters and their habits must, therefore, involve careful management of their floral resources.

There still remains a large amount of pollination biology research to be done in Australia especially in the areas of insect pollination and exploration of pollination syndromes. The arena of pollination biology also offers opportunities for the development of an understanding of many aspects of biology. For example, since the spatial and temporal patterns of nectar abundance can be accurately reassured it is possible to relate the abundance and behaviour of nectar-feeding animals to the abundance of their food. This is not so easy for the vast majority of animals that use resources that are difficult to measure. Interest in pollination biology is growing in Australia, as is evidenced by the formation last year of the Australasian Pollination Ecology Society (APES) which gives the field a promising start for the future.

UNUSUAL—BUT NOT UNIQUE

by Karen Wilson



Epacris paludosa has the pungent, pointed leaves with longitudinal or parallel veins typical of the family Epacridaceae. This family is common in the heaths of coastal and tableland Australia. It is not confined to Australia, members of it being found in Malaysia, New Caledonia and South America, but it is best developed in Australia. It is very closely related to the northern hemisphere family of heaths, Ericaceae. Photo: J. M. Baldwin.

Karen Wilson, a botanist at the National Herbarium, Royal Botanic Gardens, studies the classification of the Australian flora, with a particular interest in the sedges, family Cyperaceae, and other monocots. Here she describes in detail the differences and the similarities between Australian and European flora, points to the great number of plant species already extinct and threatened and underlies the urgent need for increasing our knowledge of Australian plant life.

"The Flora of Australia has been justly regarded as the most remarkable that is known, owing to the number of peculiar forms of vegetation which that continent presents . . . it is much easier to see peculiarities than to appreciate resemblances . . . The peculiarities of the Flora, great though they be, are found to be more apparent than real, and to be due to a multitude of specialities affecting the species, and to a certain extent the genera, but not extending to the more important characteristics of the vegetation, which is not fundamentally different from that of other parts of the globe."

So wrote Sir Joseph Hooker in his *Introductory Essay to the Flora Tasmaniae*, published in 1855. The words of this eminent English botanist, a friend and supporter of Charles Darwin, still apply today. Many people are so fascinated by the curious plants of our flora, such as the eucalypts, grass trees and grevilleas, that they overlook the basic resemblances between our flora and those of the other continents.

Australia's flora differs in many features from that of Europe. Thus the historical accident of European settlement of Australia was responsible for the flora being dubbed 'bizarre' and 'unique' by the early settlers and botanists. In addition, the unusual elements of the flora are concentrated along the coast rather than on the "sweeping plains" so that the early settlers saw the most unusual aspects of the flora rather than the inland vegetation, which is more similar to that of other continents. The impact of this "sunburnt country" on those used to "ordered woods and gardens . . . and soft dim skies", as Dorothea Mackeller so evocatively expressed it, must have been great, and certainly not favourable in many cases.

There are many species and genera, but very few families, endemic (restricted) to Australia. A satisfactory explanation of this is provided by the process of continental drift. Family ancestors are thought to have been present on Gondwanaland and Laurasia before the continents began to drift apart. Since then each continent has developed its own peculiar flora from those common ancestors. Therefore the unique elements in the Australian flora are thought to have developed since Australia became isolated from the other southern continents.

Before looking at the most characteristically Australian plants, it is useful to consider some of the features of the vegetation that are

peculiarly Australian and some of the factors that helped produce them.

Australia has more deciduous trees and shrubs than northern Europe but this is not obvious because they are mostly found in the relatively restricted and remote tropical monsoon areas of northern Australia. There are few deciduous species in the rest of Australia, where forests, woodlands and shrublands are overwhelmingly dominated by evergreen species. This contributes to the monotonous appearance so obvious, and sometimes distasteful, to European eyes used to annual renewal of leaves.

There are few species of conifer. This may seem hard to believe if one has seen the extensive cypress pine forests of inland eastern Australia but these forests consist of vast numbers of individuals of one or a few species, which is very different from saying that there are numerous species present.

The Australian arid zone has no big succulent species, unlike arid America with its cacti and southern Africa with its aloes.

Three groups (eucalypts, wattles and hummock grasses) dominate most of the Australian landscape except in rainforest and alpine areas. The abundance and diversity of these three groups is notable. Most plant communities are classified and named according to the species of these genera found there, for example, mulga *Acacia aneura* woodland, river red gum *Eucalyptus camaldulensis* forest, hummock (*Triodia* and *Plectrachne* spp.) grasslands. Each group has an unusual feature in its leaves: most wattles have their leaves reduced to phyllodes; eucalypt leaves are tough and are mostly held vertically, consequently the trees cast little shade; porcupine grass leaves have many thickened cells and other anatomical adaptations to reduce the effects of water loss. Such features can be termed scleromorphic.

Scleromorphy is common in Australian plants. The name is derived from Greek 'skleros' meaning hard or tough and Greek 'morphē' meaning form or shape, and refers to morphological adaptations in the plant which enable it to survive conditions of low moisture, high temperatures, infertile soils and/or frequent fires, all of which are common in Australia. As the term suggests, scleromorphic features are often 'tough': leathery leaves, inrolled leaves, leaves reduced to spines or tiny appendages, thick woody fruits which may



Clusters of the yellow flowers of *Acacia echinula* are typical of the biggest plant genus in Australia, *Acacia*. *Acacia echinula*, pictured left, has phyllodes that are pungent, pointed and round in cross-section rather than the flattened leaf-like phyllodes more common in Australian species.

The yellow flowers of common everlasting daisy, *Helichrysum apiculatum*, and the glossy red and black flowers of Sturt's desert pea, *Clianthus formosus*, shown below, form a vivid picture against the red soil of inland Australia. These two species belong to big cosmopolitan families, *Asteraceae* and *Fabaceae* respectively, which nevertheless have many endemic Australian members. Photos: J. M. Baldwin.



Eucalyptus tetraptera of southwestern Western Australia has large (c. 4cm in width) angular woody red fruits. The lower fruit in the bottom photograph shows the operculum or cap being shed, exposing the pink stamen filaments. These fruits are amongst the most unusual found in the big genus *Eucalyptus*, which more typically has cup or urn-shaped fruits. Photo: A. Wilson.

open to release seed only after fire. Some of the best communities in which to observe a range of scleromophic features are the coastal heaths of eastern and south-western Australia.

Physical factors have shaped the distribution of the flora as well as its features. Australia is a dry continent of wide latitudinal range and low relief, its highest ranges being concentrated along the coastal margin. Soils are often infertile, lacking in trace elements and/or of low water-holding capacity. Over one-third of the landmass is classified as arid. This vast arid zone supports relatively few species (most of which are widespread) whereas the more varied temperate and tropical zones contain many more species which often are restricted by their habitat requirements to small areas. For example, rainforest with its many peculiar and often primitive species is found only in pockets of high rainfall on the eastern slopes of the east coast highlands and adjacent lowlands. Similarly, alpine and subalpine areas have many endemic species but are restricted to the highest mountains of south-western Australia.

The Australian flora consists of about 20,000 species of flowering plants grouped in about 200 families of widely varying size: some families contain only one or two species, others contain one or two thousand.

Few plant families (about 5%) are endemic to Australia but many genera (30-40%) and the majority of species (85%) are endemic. The few endemic families are small, such as *Cephalotaceae*, with its single species, *Cephalotus follicularis*, the well-known Western Australian pitcher plant. The largest of the endemic families is *Tremandraceae*, a family of small undershrubs with 43 species in three genera. Some bigger families have most of their species in Australia with only a few species extending beyond Australia, for example *Casuarinaceae*, *Goodeniaceae*, *Myoporaceae* and *Pittosporaceae*. More commonly, families are widespread and have several centres of diversity, one such being in Australia with many peculiarly Australian genera and species. Thus some genera in the family *Proteaceae* are peculiar to southern Africa, for example *Protea*, a few to South America, for example *Roupala*, while many others are peculiar to Australia, for example *Dryandra*, *Persoonia*, *Telopea*; similarly for the families *Asteraceae*, *Murtaceae* and *Poaceae*. Other families containing a high proportion of species often thought of as peculiarly Australian include *Cyperaceae*, *Epacridaceae*, *Restionaceae* and *Rutaceae*.

Although recent interest in growing native plants has resulted in greater general awareness of our flora, the best-known trees must still be the eucalypts (*Eucalyptus* spp. and *Angophora* spp.). The characteristic sample of the Australian bush is largely caused by volatile essential oils found in various native plants such as eucalypts, *Boronia* spp., and *Plectranthus* spp. There are about 500 species of eucalypts, only about ten of these spreading naturally beyond Australia to New Guinea, Indonesia and the southern Philippines. Some species are now widely cultivated overseas for their essential oils and timber, but Australia has made little effort to cultivate them commercially. The eucalypts belong to the family Myrtaceae, which contains many well-known and easily cultivated genera such as *Callistemon*, *Melaleuca*, *Kunzea*, *Leptospermum*, *Chamelaucium*, *Baeckea*, *Agonis* and *Syzygium*.

Acacia is the biggest genus of trees and shrubs in Australia. It includes about 1,000 species, which are commonly called wattles. Like the eucalypts, wattles are found in most plant communities and, in the arid zone, are more common than eucalypts. About 80% of the species of *Acacia* are found in Australia, although *Acacia* spp. are widespread in the tropics and subtropics of America, Africa and Asia. Thus the main concentration of species is here. Nearly all the Australian species are closely related to each other and only distantly related to those found elsewhere. Some Australian species have bipinnate leaves but most are phyllodinous, meaning the leaves have been reduced in the course of evolution to a flattened petiole (phyllode) which looks like a simple leaf. *Acacia* is the biggest genus in the family Mimosaceae.

The three legume families, Mimosaceae, Caesalpinaceae and Fabaceae, are found on all continents but have numerous genera with endemic Australian species. *Acacia* has already been mentioned. In the tropical and arid zones *Cassia* (family Caesalpinaceae) is a common genus of shrubs. Only about 15% of genera in the family Fabaceae are found in Australia and even fewer are endemic. However the tribe Podalyrieae contains a group of endemic genera (for example *Pultenaea*, *Jacksonia*, *Chorizema*, *Daviesia*, *Dillwynia*) which are very common especially in the heathlands. In the Fabaceae are such well-known plants as Sturt's desert pea *Clianthus formosus*, black bean tree *Castanospermum australe*, native sarsparillas *Hardenbergia* spp., native wisteria *Millettia megasperma* and darling peas *Swainsona* spp.

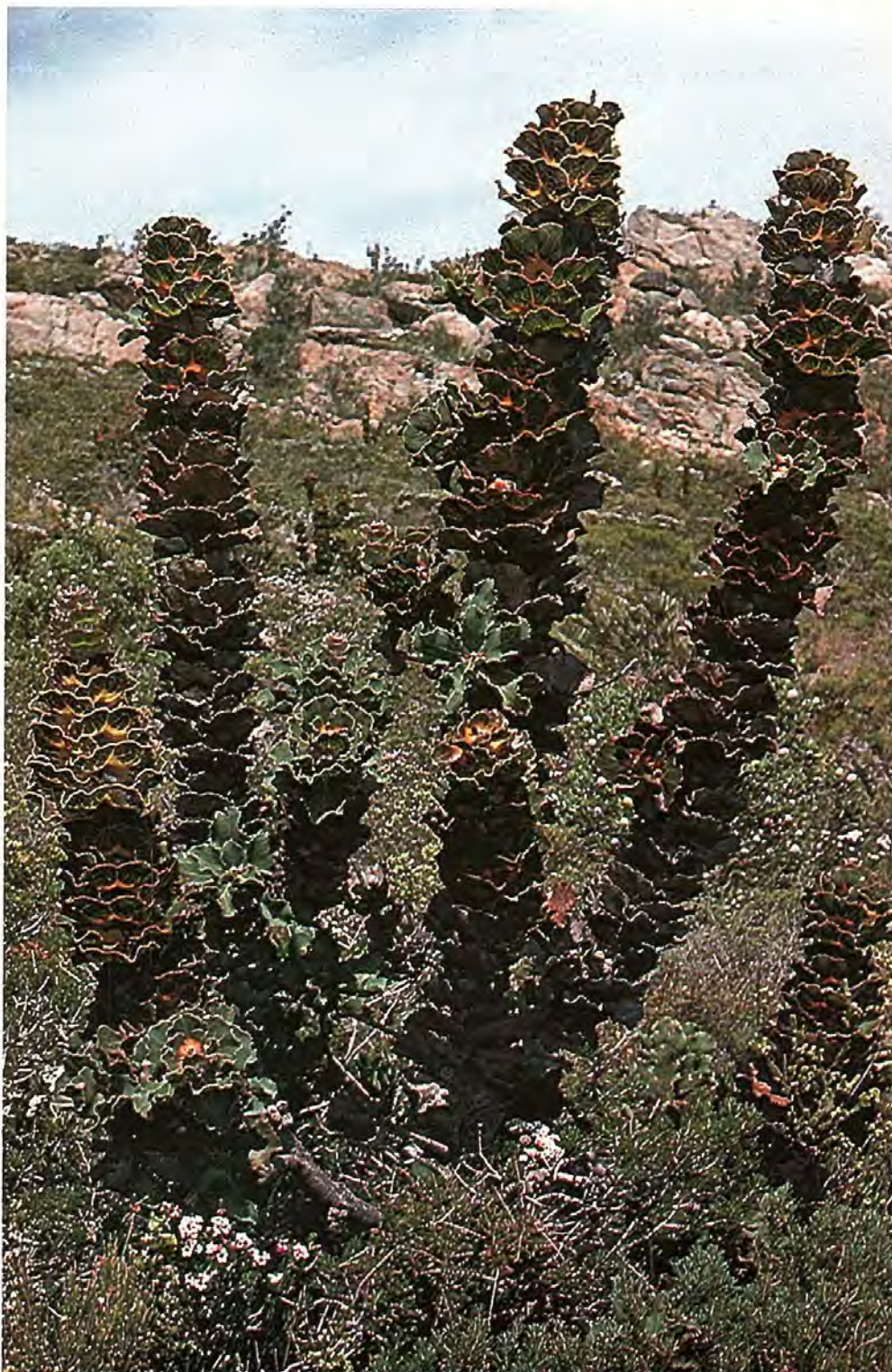
Legumes are able to 'fix' atmospheric nitrogen by means of bacteria living in root nodules. This adaptation enables these plants to supplement their supply of nitrogen, which is often inadequate in Australian soils. In recent years other plants have been found to fix

nitrogen, sometimes due to bacteria but sometimes due to cyanobacteria (blue-green algae) or fungi in root nodules. Such plants include *Casuarina* spp. and *Discaria pubescens*.

Another adaptation to overcome nutrient problems in low-fertility and often swampy soils is shown by the insectivorous plants, which trap insects for food. Such plants are not confined to one family but rather are found in several, such as the Nepenthaceae (tropical pitcher plant *Nepenthes mirabilis*),

Droseraceae (sundews *Drosera* spp.) and many Lentibulariaceae (*Utricularia* spp., fairy aprons or bladderworts). They are not exclusively Australian although many species are found here.

The family Casuarinaceae has its centre of diversity in the heaths of eastern and south-western Australia. All the Australian species are endemic, except for *Casuarina equisetifolia* which is found naturally beside tropical beaches from Bangladesh to Malesia and the



Hakea victoriae (family Proteaceae) is a striking member of the heath community on East Mt Barren in Western Australia. Its long stems, with their large prickly variegated leaves, rise to 2.5 metres. Members of the family Proteaceae are especially common in such heaths, both in Australia and South Africa. Photo: A. Wilson.



Male and female flowers are borne in separate inflorescences in the family Casuarinaceae. Male inflorescences are long and slender; female inflorescences form small red-brown clusters at first but then develop into woody cones. The true leaves in she-oaks are reduced to a ring of tiny teeth around the green branchlets. Photo: J. M. Baldwin.

Pacific islands. One genus, *Gymnostoma*, has only one species in Australia but has sixteen others scattered from Malesia to New Caledonia. Trees and shrubs in this family are commonly called she-oaks, in reference to the similarity (but inferiority for wood-working purposes) of the timber to that of the English oak. 'She' in common names often indicates the supposed inferiority of the named species or its attributes to that of the compared species!

Some families have few endemic Australian representatives but those that are well-known deserve brief mention. Flannel flowers belong to the only widely known native genus (*Actinotus*) in the family Apiaceae, which has 275 genera worldwide (including such common food-plants as the carrot and parsley) and nine genera endemic to Australia.

Another such family is Sterculiaceae, a mainly tropical family, which has less than 40% of its genera and species native here. This figure includes the genus *Brachychiton*, which has such species as the Kurrajong, *B. populneus*, Queensland bottle tree, *B. rupestris* and flame trees, *B. acerifolius* and *B. diversicolor*. Similarly the family Meliaceae is widespread in the tropics and subtropics with few Australian endemics but is well known here because it includes the white cedar, *Melia azedarach*, and red cedar, *Toona australis*.

Nearly all the examples of characteristically Australian plants mentioned so far have been drawn from the dicotyledonous plants (dicots), partly because there are about three times as many dicots as monocotyledonous plants (monocots), but also partly because the dicots are more widely known. Many of the monocots are botanically interesting in their structures and distribution, but they are generally less showy than the dicots and hence tend to be overlooked. Notable exceptions are the grass trees, *Xanthorrhoea* spp., kangaroo paws *Anigozanthos* spp., Gynea lily *Doryanthes excelsa* and fringed lilies,

Thysanotus spp. Most monocot families such as the palms and orchids have their major centres of diversity elsewhere and have relatively few representatives here. *Archontophoenix*, *Carpentaria* and *Normanbya* (all palms) and *Caleana*, *Rhizanthella* and *Drakea* (orchids) are some of the few endemic genera in those two families mentioned.

Grasses (family Poaceae) are perhaps more common in terms of plant numbers than other monocot families, but they also have few endemic genera here. Probably the best-known grasses are *Triodia* and *Plectrachne*, which are two closely related endemic genera widespread over large areas of arid Australia as hummock grassland. They are commonly called porcupine grasses or spinifex, although the latter is discouraged since *Spinifex* is the botanical name for a common sand-binding grass found on coastal sand-dunes. Many grass species are endemic and are often very widespread, such as kangaroo grass, *Themeda australis*. Grasses are considered to have diversified more recently than many of the dicots and this is reflected in their distribution pattern. The worldwide distribution of the grasses differs from that of most other widespread families in that no continent has a great concentration of endemic genera. Their distribution within Australia also differs from that of other families in that the arid zone has a higher proportion of endemic grass groups than other regions.

This brief account of the Australian flora has concentrated on the flowering plants (angiosperms), which are generally the most conspicuous and most abundant elements in the Australian landscape. However, it would not be complete without some mention of the Australian gymnosperms and ferns and the simpler and more primitive non-vascular plants such as mosses and algae.

The gymnosperms, ferns and fern allies are vascular plants like the angiosperms but

are far fewer in number (only about 500 species in 140 genera in Australia) and are non-flowering and more primitive than angiosperms. The gymnosperms include two very different groups: the cycads (for example, the Burrawang), which are palm-like in appearance, and the conifers (for example, the cypress pines, hoop pine and celery top pine). Half of the Australian genera and about 80% of the 80 species are endemic. The species often have very narrow ranges: an extreme example of this is the conifer *Microstrobos fitzgeraldii* which only occurs on cliff faces near a few waterfalls in the Blue Mountains of NSW. The ferns and allied fern-like groups are far more numerous than the gymnosperms. About 50% of the species are endemic, including the tree ferns *Dicksonia antarctica* and *Cyathea australis*, the Elkhorn *Platyserium bifurcatum*, and most species of Nardoo, *Marsilea* spp.

The non-vascular plants are generally small and readily distributed. Hence they tend to be cosmopolitan and there are few genera and species endemic to Australia. The Australian representative and their relationships are mostly less well known scientifically than the vascular plants.

Although the Australian flora has been studied for about 200 years, our knowledge of it is still far from complete; indeed, numerous species remain unnamed, particularly in tropical Australia. As we lack even a basic inventory of all our species it is, then, hardly surprising that little is known about the biology of particular species or the detailed requirements for their conservation.

It has been estimated that about 70 plant species are probably already extinct, and at least 500 species are currently threatened with extinction in Australia. It is to be hoped that knowledge of our remarkable flora continues to increase—before the threat becomes reality.

FURTHER READING

- Australian Natural History*: articles in various past issues: on palms (vol.17:21-26), on insectivorous plants (vol.18:1-5), on epiphytes (vol.19:112-117), on botanical exploration (vol.19:57-61), on heathlands (vol.20:111-116).
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OUR PHOENIX FLORA

Bush-fires are a familiar part of the Australian scene, and since the so-called 'development' of this country by white settlement are widely regarded as a fearsome menace. Ross Bradstock, a post-graduate student in the School of Biological Sciences, University of Sydney is currently carrying out research on the dynamics of shrub species under varying fire regimes. In this article he raises some little-known but challenging ideas on the benefits of fire in the conservation of Australia's flora and vegetation, and points to the need for informed control management.

by Ross Bradstock



The fearsome grandeur of an Australian bushfire is dramatically caught in this photograph. Widespread destruction of life and property frequently follow such outbreaks, yet the natural frequency of fire has a precise role to play in the perpetuation of much of the distinctive Australian bush. Photo courtesy NSW Parks

A well worn platitude likely to be heard in many discussions of bushfires is that 'Australian plants are adapted to fire'. What is consciously or unconsciously meant is that some species are able to flourish under frequent burning and the ability to resprout from burnt stems or the retention of seeds in woody fruits are held as evidence of this. Conversely, some types of vegetation such as rainforest are described as 'fire-sensitive'.

This attitude obscures the fact that species readily survive and reproduce under a whole range of different types of burning and, indeed, species with no obvious 'fire adaptive' features or resistance to fire are actually dependent on it for long term survival.

To understand fire effects we must consider the adaptation of species as a whole, not just the individual features of plants. We must understand the life history strategy of any given plant species, which is its plan for continued survival as determined by particular characteristics in each phase of its life-cycle. In relation to fire this means considering its effects on the vegetative and reproductive phases of established plants and on the seed and germination phases. Furthermore, we must view fire not as an intermittent accident or catastrophe, but as a disturbance with a regime of frequency, intensity and seasonal occurrence. Species are adapted to survive and reproduce under certain fire regimes and may be dependent on them for continued survival.

Fire effects can be resolved into a limited number of outcomes at each stage in a species life-cycle. The means by which these outcomes are achieved are varied and diverse, but what is important in linking fire regimes to species is the end result.

Plants can either survive a fire in part or whole, or die. Survival implies that some live tissues, capable of initiating fresh growth, are shielded from the lethal temperatures generated in a fire. Protection of these tissues is interdependent on the plant's anatomy and morphology and fire intensity and must be sufficient to prevent cells experiencing temperatures of about 60°C or more for longer than a couple of minutes. Insulation can be provided to aerial buds by both live and dead tissues such as bark and for buried buds, by the soil. Not all plants possess both methods, monocotyledons, for example, are mostly reliant on recovery from buried buds only. Depending on the habitat of the plant, be it tree, shrub or herb, fire damage will tend to be most severe on the smallest and lowest in-

dividuals. As a rule of thumb, herbs and small shrubs, if they are able to survive, will tend to recover from underground buds, on the stem, roots or rhizome. Larger shrubs and trees if their foliage is damaged recover from protected buds in the stem and branches; often they will possess undergrowth recovery mechanisms as well. Most species can be thought of as having a maximum fire intensity tolerance determined by the intrinsic amount of bud insulation. This tolerance will vary in a population due to variations in size and age of individuals. The tolerance of some species may be so low as to render them susceptible to virtually any fire. As well, some species may lack buds capable of regeneration. These may be called 'fire sensitive' species.

The effects of fire seasonality and frequency are not well known but a general argument can be made out that individuals which are burnt very frequently are likely to die. As recovery is dependent on stored reserves which are not supplemented until significant numbers of new leaves are produced, very high fire frequencies may cause depletion of these reserves before they can be replenished. The critical frequency for any species will depend on its rate of production of new leaves. Production of a healthy crop of new leaves may be a matter of weeks for some grasses, or some months in, for example, *Eucalyptus* trees with full crown recovery taking even longer.

An important part of vegetative recovery is the time taken for flowering to recommence, or in the case of burnt juveniles, first commencement. Fire frequencies less than this time will prevent species from producing new seed and hence prohibit the addition of new individuals to the population.

It is convenient to think of seeds in terms of populations, just as we think of populations of established plant. We can call a species seed population its 'seedbank', implying by analogy that this is the way a species 'invests' in its future survival.

At any point in time most species have a stored 'seedbank' at the sites they occupy. However, in some there is a crucial juvenile period when little or no seed exists. The storage of the seedbank occurs in basically two forms: in the soil layers, or in the fruits held above ground. Some species, as they age, will accumulate most of their seeds in the fruits; for most the seeds are continually released as produced (though the time of release varies greatly with species) and incorporated into the soil. It is the fate of the seeds



The aftermath of a very high intensity wildfire, top. Epicormic shoots are beginning to sprout five months after the burn, but germination on the bare ashbed is yet to commence. Photo A. Fox, courtesy NPWS.

These burnt *Hakea* fruit have split open and shed their seed. The thick wood of the fruits gives excellent insulation to the seeds. Photo A. Healy.

Two forms of vegetative recovery from fire are shown here. Top right gives a good example of epicormic shoots in *Eucalypts* and lower left resprouts from roots in shrubs. Photos R. Bradstock.

once they enter the soil which is important with regard to fire. Some species have seeds with dormancy mechanisms which enable them to survive for varying lengths of time. Others are effectively lost soon after they reach the ground. For these the effective seedbank is that carried in its fruits at any given time, usually the product of one or two seasons of flowering.

Survival of the seedbank during fires depends on the insulation of fruits and/or the depth of burial in the soil and fire intensity. Fruits stored further from the ground will tend to escape many fires, while smaller life-forms will rely on burial and dormancy or heavy fruit insulation. However, some species possess none of these features and any seedbank will usually be destroyed forcing re-establishment of the species to be dependent on the ease and rate of seed dispersal from unburnt sources.

Some critical fire intensities will render a species seedbank inviable according to the amount of insulation or burial that is characteristic of the species. Depth of burial is important in determining survival of buried seed while thickness of cones, capsules, follicles or other fruit structures will affect survival of seeds above-ground. Features which confer little or no fire resistance, such as light or hairy seeds borne in open heads, may facilitate dispersal. Other well insulated seeds can also have 'wings' which enable some dispersal on release.

Provided seeds are available, post-fire conditions are usually optimal for germination as fire disturbance creates an open environment. Light, water and nutrients are usually more readily available and for a time the amount of space open for a germinating plant is unlimited. Fire therefore assumes additional importance for many species able only to germinate and establish in disturbed conditions. We may call these species 'intolerant' as opposed to those 'tolerant' ones which can establish in undisturbed conditions. What are the reasons for 'intolerance'? Some species seem able to germinate in any light conditions provided moisture is available. In the reduced light under a developed canopy of foliage, however, they may fail to establish. Another inhibitory mechanism is 'allelopathy'. Toxic or inhibitory (allelopathic) substances, given off by live individuals or the litter of some species inhibits germination and/or establishment of their own or other species. Fire destroys or

neutralises the chemicals responsible by baking the upper soil and renders the ashbed non-toxic. This mechanism has been demonstrated for some species of the Californian chaparral vegetation (a very fire-prone community) and is often invoked as being a feature in Australian species, but its existence has only been demonstrated in blackbutt *Eucalyptus pilularis* and silky oak *Grevillia robusta*.

Fire also directly stimulates the germination of some species by breaking the dormancy of their seed. The best examples are the legumes, including such genera as *Acacia*, *Dillwynia*, *Kennedia*, *Daviesia*, *Pultenea* and many others. Many legume seeds have a hard seed coat which, when broken by heat or other disturbances, allows the seed to imbibe water and germinate. Because of the dormancy mechanism, these seeds can be very long-lived and if fire frequency is low or they escape heat, their viability may remain for many years after the parent plants have disappeared. Fire intensity will determine what proportion of the dormant seedbank will germinate.

Very hot fires may generate heat to a depth that will affect most seeds. Other species occur with buried seedbanks which have no special dormancy mechanism. Germination may be triggered by increased soil temperatures caused by greater incident solar radiation at the burnt soil surface. Individual seeds in this sort of seedbank may be shorter-lived than the legumes. Other effects of fire, intensity, seasonality and frequency will depend on the way these variables alter the physical events which control germination. For example, some species have an optimal range of ambient temperature for germination, hence the season of burn may influence the response and overall abundance of seedlings. Differing fire intensities and frequencies may affect the quality and quantity of ash and hence mineral nutrition. Current arguments concerning the type and frequency of burning under extensive forestry practice, for example, has revolved around these hypotheses, but at present published data are lacking which would adequately settle the debate.

Germination following a bushfire may exhaust the seedbank of a species. This tends to happen in species with fruits that retain seeds until opened by a fire. If all seeds are released their subsequent germination will exhaust the seedbank.



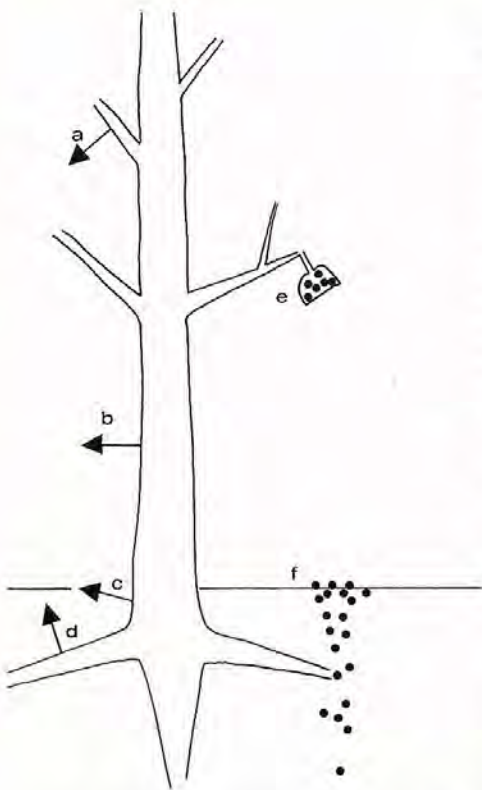


Figure 1. The position of buds from which vegetative recovery may occur after fire: a) and b) are aerial buds in the branches and stem of woody plants and at the base of leaf sheaths in non-woody species; c) and d) are subterranean buds on the stem (e.g. lignotuber in many woody species), roots and rhizomes. Protection of aerial buds is dependent on woody or pseudo-woody tissues, whilst the depth of burial of subterranean buds is crucial. Different seedbanks e) aerial, and f) in the soil, accumulate in various species. The pattern of seed shed from fruits shown at e), and longevity of shed seeds determine where the seedbank accumulates. Depth of burial of dormant seeds in the soil is important in determining seed survival during a fire, the degree of heat stimulation, and whether the new shoot will reach light. The insulation properties of fruits and their position in a fire will influence the viability of fruit retained in seeds.

As a result of various patterns of seed germination, seed longevity, flowering time and a plant's overall ability to survive, different species react to fire differently. Some examples of particular species' response to fire regimes is therefore necessary to fully understand fire effects.

Mountain ash, *Eucalyptus regnans*, the world's tallest hardwood, is an inhabitant of cool, moist forests in Victoria and Tasmania. It is easily killed by the infrequent but high intensity fires that devastate this forest type, having a thin bark and lacking the subterranean lignotuber which enables many other *Eucalyptus* species to resprout. Seed is normally produced annually and shed several years after flowering, so that at any time a year or two's crop is held in the capsules. Except when fires crown, the seedbank is mostly intact after a fire and enormous numbers of seeds are eventually dropped onto the ashbed. Germination can be equally prolific and growth of seedlings is rapid. Any ungerminated seed loses its viability rapidly, so that seedbank is effectively exhausted at each fire. Therefore, the period until first flowering of the seedlings, 15 to 20 years after germination, is critical; a second fire in this time will kill the young seedlings and saplings, and, as there will be no seedbank, the species will be eliminated. Conversely, if the population remains unburnt the even-age stands grow and develop until after around 400 years the population has thinned out to a few enormous individuals which dominate the dense understorey of rainforest species. If no fire occurs these remaining trees age and die and as no germination is possible, the species is lost.

A fire frequency of between 20 and 400 years is essential and high intensity fires give the best germination and conditions for fast

Examples of seed: from the top, right, isopogon seed, winged banksia seeds, *Acacia* seeds with hard seed coat and elaiosome. Photo R. Bradstock

Germination in open conditions after fire, lower right. Photo by Ross Bradstock

growth. Fires in late summer are best, as this is the usual time of seed shed. A later fire will mean that little seed will be available and freshly shed seed will be consumed. Under these conditions germination will be delayed until the cold winter is over and this may allow bracken, *Pteridium esculentum*, and other resprouts a head start, which will choke seedlings and result in poor growth.

In contrast, the familiar and often quoted heath banksias, *B. ericifolia* and *B. ornata* live 30 to 50 years and, unlike *E. regnans*, store virtually all the seed they produce in cone-like fruits held on the branches, allowing the seedbank to increase with age. Fire causes widespread death of plants and release of seeds. Although a small proportion is released between fires, this is ineffective in producing new established plants in unburnt conditions. In *B. ericifolia*, the seasonal timing of seed release and germination has been found to be important, with a higher probability of successful germination and establishment occurring in autumn-winter than in summer.

As the species considered all respond in an identical manner to fire it is important to consider the comparative life history patterns. The difference in longevity between banksias and mountain ash shows that a different fire frequency is required, 5-50 years versus 20-400 years, but to simply categorise the banksia species as fire adapted and the mountain ash as the opposite is wrong. All have the same reliance on fire but are adapted to different fire regimes.

Both *Acacia suaveolens* and *B. ericifolia*, which are often found near each other in dry shrublands or forests, can be used to show different attributes of a persistent seedbank and modes of vegetative recovery. *Acacia suaveolens*, a legume which does not live for more than 15 years, typically stores its hard-coated seeds in the soil. Germination occurs best after hot fires and in contrast, very cool burns may leave the seeds intact, resulting in little or no germination. Seeds are probably longer lived than the parent bushes so if a fire does not occur after the latter have died, the





species exists as an underground population of seeds. The longevity of these seeds is unknown but burns in thirty-year-old vegetation have resulted in fresh germination of *A. suaveolens* although the species had apparently been absent for many years. As the species usually begins flowering the second autumn after germination, there may be tolerance of high fire frequencies down to a five-year cycle. More frequent fires than this will rapidly deplete the seedbank before fresh seeds can be incorporated into the soil. Similarly, in the mountain ash forests, *Acacia melanoxylon* follows the same pattern but lives approximately 50 years as a tree and its seed for up to 500 years.

The ability to recover vegetatively causes species populations to be composed of multiple age classes. As a general principle the ability to recover enables species to be tolerant of a wider array of fire frequencies. Considering the spectrum of life-forms from trees to shrubs and herbs and grasses, it can be seen that very high fire frequencies will favour a herbaceous habit and the capacity to resprout rapidly from roots and rhizomes. A good example is bracken, *Pteridium esculentum* which is able to survive under annual burning, due to its extensive and vigorous rhizome and the ability to produce spores each year. This species can dominate large areas under this type of burning, recovery starting within weeks of a fire and being complete within months.

On the other hand, we can consider tall, moist forest trees such as messmate *Eucalyptus obliqua* or blackbutt *E. pilularis* which have a degree of fire tolerance from a stocking of rough bark on the trunk, the ability to resprout from epicormic buds, and a degree of shade tolerance in the young seedlings and saplings. Stands of these trees may have several age-classes, ranging from dominants down to small saplings, each dating from different fires. Established trees will survive cool to medium fires and if, in the example of blackbutt, these coincide with seed shed, good germination may follow. A fire cycle down to five years may be tolerated by young and old trees alike, if these burns are of low intensity.



The logical extension of this approach is to consider assemblages of species, that is, vegetation types or plant communities. Of particular importance is the attribute of tolerance, that is, the ability to establish and grow in the presence of like or different species.

In the example of a moist, Tasmanian forest dominated by *Eucalyptus regnans*, when the eucalypts senesce and die, 400 plus years after fire, the forest type changes from sclerophyll to rainforest, with principally a mixture of Antarctic beech, *Nothofagus cunninghamii* and sassafras *Atherosperma moschatum*. Like the eucalypt these species establish after fire but their growth is slower and in the first 50 years they are dominated by eucalypt, *Acacia* and other shrubs and small trees. However, they can tolerate shading and root competition so persist and eventually dominate due to sheer longevity. *Atherosperma* seedlings may germinate and establish under an old rainforest canopy. *Nothofagus*, on the other hand, needs a fire to establish but will do so on a longer cycle than *E. regnans*. Conversely, fires about every 50 years will result in a perpetuation of a wet sclerophyll forest type composed chiefly of several dozen species as opposed to the two or three angiosperms present in an old *Nothofagus* rainforest. This pattern of species diversity is typical of many vegetation types, there being a decline in diversity as time elapses after a fire. This is often the reason given to justify a frequent burning policy to maintain diversity. The 'decline' may be more apparent than real and for a number of species, whether they be in a heath or moist forest community, it represents the reversion to the dormant seed phase as established individuals die out.

Fire management, be it for economic values as in commercial forests, nature conservation, national parks and wilderness areas, or for the protection of society, must be based on the concept of fire regimes. Managers being faced with multiple objectives, unexpected events and the need to make rapid decisions need use of a system of species attributes facilitating the modelling of plant communities and their behaviour. The integration of these models with data on fuel



Banksia ericifolia heath (centre) and *Eucalyptus regnans* with rainforest understorey (above), make a striking comparison, yet each dominant is equally dependent on fire although different fire regimes are needed for each. *Pteridium* or bracken thrives under a very high fire frequency as the photograph left shows, the picture was taken only a short time after fire.

accumulation, fire behaviour, meteorological conditions, topography and species distributions can be made using computer programs which allow rapid assessment of different fire management options. Such a scheme is being developed in Kosciusko National Park.

The choice to burn or not burn any given piece of vegetation can be made in ignorance or with regard to available knowledge about fire effects on plants. Arguments concerning what constitutes 'natural', 'past' or 'primitive' fire regimes are often irrelevant. We need to understand how species behave and tailor management plans and objectives accordingly.

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FISH BEDS REVEAL LUSH FOSSIL FOREST

Whenever anyone mentions fossils most people immediately think of static impressions of plants and animals in rocks and not the active type of environment which produced them. The Talbragar Fish Beds in central NSW is one such site, where fossils show evidence of a pre-existing lush forest of kauri pine in what is now dry scrubland. World famous for the fossils it has produced, Talbragar Fish Beds date from 150 million years ago and was the site of a reasonable-sized lake. Mary White, a Research Associate of the Australian Museum, is actively engaged in the study of fossils from this site and is presently curating the plant fossil collections of the Australian Museum and the Geological and Mining Museum.

by Mary White



Foliage spurs of *Agathis jurassica*, a kauri pine of Jurassic age and the leaves of *Pentoxylon australica*, an arborescent cycad. Photo David Barnes.

In many countries of the world there are famous fossil sites which excite the interest and capture the imagination of the general public as well as palaeontologists by enabling them to glimpse the remote past as the living reality it once was. The Talbragar Fish Bed locality in NSW is such a site.

Located northeast of Gulgong in eastern central NSW, the Talbragar Fish Bed is world famous not only for the beautifully preserved fossil fish remains it has produced, *Leptolepis*, *Coccolepis*, *Archaeomene*, *Aetheolepis*, etc., but also for the wealth of associated fossil plant remains. The latter are usually preserved as white impressions in an ochre-coloured silicified shale. The shale deposit, of very limited extent and outcrop, represents fine-grained sediments which accumulated in a late Jurassic lake about 150 million years ago. Its still waters and presumably, anaerobic sedimentation conditions (without oxygen) provided ideal conditions for the preservation of the fish and plant remains which accumulated in the bottom muds.

The beautifully preserved fossil specimens which occur in the finely laminated rock are well known to, and much sought after by, fossil collectors. As a result the shale lens has been extensively excavated and almost quarried out since it was first discovered in 1889 by A. Lowe of Wilbertree, NSW. The remaining shale outcrops have been declared a geological monument to protect the site from further destruction and there are penalties for anyone found removing material from it.

Fortunately large quantities of Talbragar Fish Bed material have ended up in the Geological and Mining Museum, the Australian Museum and other institutions, but the material available for study represents only a small part of the shale lens. Many specimens remain in private hands and make no contribution to knowledge of what has proved to be a most significant fossiliferous horizon.

When the first specimens were seen in Sydney in 1889, the then Geological Surveyor of NSW, William Anderson, arranged for the Mines Department fossil collector, Charles Cullen, to go and quarry out a large collection of specimens. Bearing in mind the remoteness of the Talbragar River area in those days and the lack of transport and other facilities, it must have been quite an expedition. The task of bringing back many tons of rock samples by

bullock or horse-drawn cart to the nearest railhead at Mudgee was not to be undertaken lightly. Mr Anderson himself visited the site that year and wrote an official report to the Mines Department describing his visit and the "very large numbers of specimens which were awaiting transportation".

These specimens which were obtained mainly from the "splitting up of the oblong and square blocks which lay scattered over the surface of the hill" and not from the excavation of the underlying bed in the hillside, are the Cullen Collection, and remain as an unbroken collection today. That they do so is largely because space was always at a premium in the Mines Department and after an initial examination to select representative material from all the different species present for study the bulk of the specimens remained crated and in storage.

In 1890, a plant list compiled by Robert Etheridge, the then Director of the Australian Museum and W. S. Dunn, the Government Palaeontologist, was published, identifying the species by comparison with species described in the palaeobotanical literature of the day. They listed *Taeniopteris daintreei*; *Podozamites lanceolatus*, *P. spathulatus*, *P. longifolium*, *Thinnfeldia odontopteroides*, *Taxites planus*, *Neuropteridium australe?*, and *Sphenopteris* sp.

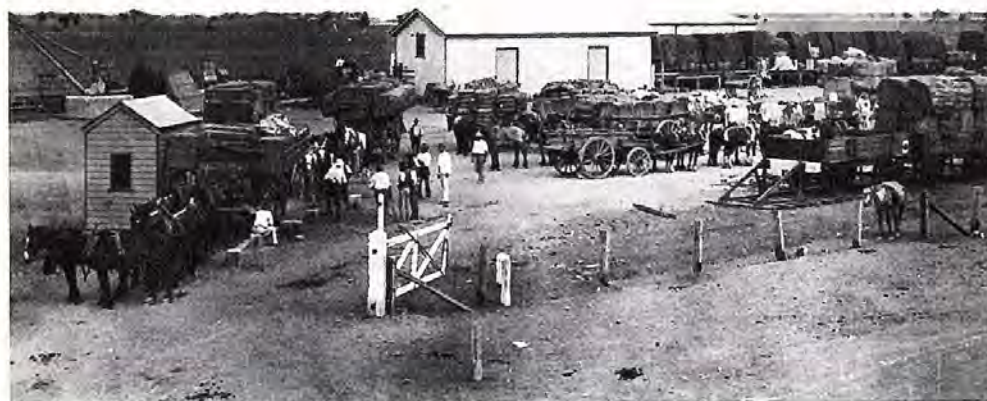
The same selection of plant specimens was re-examined by Dr A. B. Walkom in 1921, without reference to the bulk of the collection. He identified *Podozamites lanceolatus*, *Taeniopteris spatulata*, *Elatocladus planus*, *Cladophlebis australis*, *Coniopteris hymenophylloides*, *Thinnfeldia pinnata* n. sp., *Thinnfeldia talbragarensis* n. sp., *T. feistmanteli*, *Araucarites grandis* n. sp., ? *Brachyphyllum* sp., and ? *Pagiophyllum peregrinum*.

A representative selection of the fish species were sent to A. Smith Woodward at the British Museum in 1890, and his monograph, published in 1895, remains a standard reference on the fauna.

The Cullen Collection crates made of rough-hewn wood with handmade nails, with the specimens wrapped in 1885-1890 newspapers and packed in wheat straw with grain still attached, were stored for years at the



Top left, foliage spur (0.7 natural size), top centre, young female cone (3x natural size) and top right, mature cone scale (approx. natural size) of *Agathis jurassica*.



Left, a typical inland railhead of 1890 with wagons of the type which would have been used to cart the specimens from the Talbragar site. Photograph courtesy the Macleay Museum, Sydney.

Mines Department's Londonderry Depot near Penrith, as shortage of storage space at the Mining Museum in George Street necessitated their removal.

The collection was returned to the Mining Museum when a complete revision of the flora was undertaken. The revision was inspired in the first instance by the purchase of a specimen by the Australian Museum containing a cone of then unknown affinities. No cone like this had ever been seen before and it was necessary to examine all available Talbragar material to establish whether it was the cone of any of the plants previously recorded from the Fish Beds.

The specimens which had been selected in 1889 to show the representative species and which were reported on by Etheridge (1890), Woodward (1895), and Walkom (1921) combined with what was stored at Londonderry, comprise the total Cullen Collection of 1889. Therefore it has been possible to make an assessment of the relative proportions of the species in the assemblage.

Mr Cullen, a most careful and conscientious collector, kept and packed the smallest fossiliferous fragments obtained by splitting the large blocks of shale which were exposed

near, or quarried from, the shale lens. When the selection was made from the collection in 1980, the less common elements were extracted in order to show all the species present and the resulting museum collections gave a false impression of the composition of the plant assemblage. This is always a danger in museum collections as opposed to bulk field collections.

Using a somewhat arbitrary system of determining 'occurrence' of a species, it was found that in the approximately 5000 specimens of the Cullen Collection there were 1300 occurrences of *Podozamites lanceolatus*, 1060 of *Taeniopteris spatulata*, only 75 of *Elatocladus* type conifer foliage, and 24 examples of two lesser conifers. There were 3000 occurrences of pteridosperm fronds (*Thinnfeldia*) and 37 fern frond fragments, one cycad frond and one herbaceous lycopod. Thirteen reproductive structures were found which relate to the *Podozamites* foliage, and eight to the *Taeniopteris* leaves. No additional evidence was found of insects, the original ? *Cicada lowei* described by Etheridge and Oliff in 1890 remains the only one found at Talbragar. There were no feathers and the only bones were those of the fish which are present in such large numbers.

Because so many specimens are available to study, and because the fossils are so excellently preserved and diverse, it has been possible to obtain a full understanding of some of the plants. In palaeobotany one is almost invariably dealing with fragmentary evidence. Good, well preserved leaves, for instance, are seldom connected to a stem or to a fructification. Where a cone is found attached to a stem it is rare to find foliage attached to show beyond doubt the relationship of the different organs. The common association of both vegetative and reproductive organs in the same bed is often the only evidence of relationship. In the Talbragar material we are far more fortunate and the evidence on which the major species are now classified would pass the tests modern botanists apply to living plants.

When Etheridge called the commonest plant *Podozamites lanceolatus* he matched it to a specimen illustrated by Lindley and Hutton from Britain, and implied that the characteristic twigs with many leaves were pinnae of cycad with pinnules. Although Walkom realised the conifer affinities of the plant, he did not change the name. He found and described an araucarian cone scale but was not in a position to decide which foliage it was related to.

The beautiful cone *Rissikia talbragarensis* has leaves of *Elatocladus* (*Taxites*) *planus* attached, and similar foliage is now known to belong to the family Podocarpaceae. The arrangement of the seeds and scales in the cone confirm its affinity with that group of

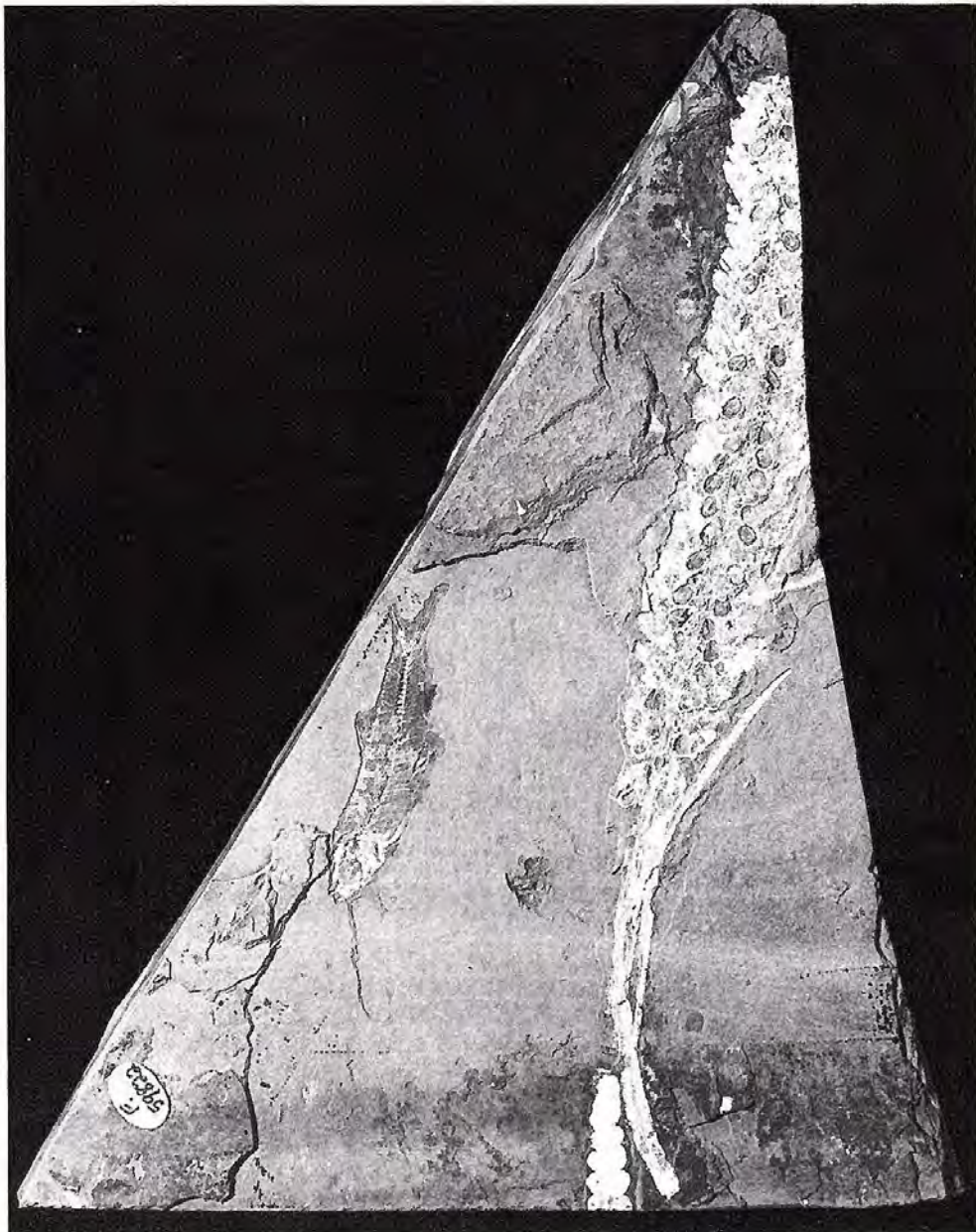


Right, cone of *Rissikia talbragarensis* (Podocarpaceae), the specimen which inspired the revision of the Talbragar fossil finds. (Two-thirds natural size.)

Above, the foliage of *Rissikia talbragarensis*. (Two-thirds natural size.)

conifers. Close examination of the Cullen Collection yielded one more fragment of a *Rissikia talbragarensis* cone which on its own would not have been determinate, but which even shows some features of seed attachment which were obscure in the complete cone; and one specimen containing free seeds from such a cone.

The many large cone scales found in the Cullen Collection, and subsequently in other collections, are araucarian in character. The Aracariaceae has two genera, *Araucaria*, monkey puzzles and Norfolk pines, and *Agathis*, Kauri pines. An examination of living *Agathis* trees shows that *Podozamites lanceolatus* from Talbragar is also *Agathis*. The leaf litter below *Agathis* trees in the Royal Botanic Gardens, Sydney, would make a suite of fossils the same as that which occurs in the Talbragar Fish Beds. It consists of large numbers of foliage spurs, each of a number of leaves, and complete ones show scales at the base from the overwintering bud. The young spur grows through the scales in *Agathis robusta* and they remain loose but encircling the stem. Talbragar spurs show markedly swollen bases with scales in many instances. Deciduous spurs are a characteristic of some modern conifers like *Metasequoia* as well as *Agathis*.



Young *Agathis* female cones tend to abort and the leaf litter contains immature cones of different sizes with crowded scales. The young araucarian cones which occur in the Talbragar material are similar in appearance. Rare pollen cones, which are papery and delicate, occur in the leaf litter, and resemble the two examples of such cones identified in the fossils. Mature *Agathis* female cones explode into constituent parts when they fall, and their large, broad cone scales with central depression for the seed are scattered in the leaf litter. Only the characteristic single-winged seed is missing in the Talbragar case. The fact that numerically the commonest reproductive structures relate to the commonest foliage adds weight to determination of the scales as *Agathis*.

In the case of the *Taeniopteris spatulata* leaves in the collection, their re-determination as *Pentoxylon australica* sp. nov was made without any room at all for doubt as a result of

evidence in the Cullen Collection. The cones which Walkom had described in 1921 as 'Conites' proved to be the 'mulberry-like' fruits of *Pentoxylon*, a Jurassic cycadophyte. One of the cones described by Walkom has not yet been relocated in the Mining Museum, but the other occurs as a deep natural mould. A latex cast reveals a little bunch of seeds. The seeds are in whorls of five on the central axis, attached to it without stalks. They were originally embedded in fleshy material.

Fruits of this sort described from India are called *Carnoconites*. The Indian material is in the form of petrifications of stems, leaves and fruits. The stems show the multi-stellar arrangement of *Pentoxylon*, the leaves are *Taeniopteris spatulata*, and the *Carnoconites* fruits are undoubtedly from the same plant. In Australia *Pentoxylon* stems occur petrified in Queensland, and *Taeniopteris spatulata* leaves are widespread in Jurassic and lower Cretaceous strata, so identification of the fruits enables the establishment of a new species—



Pentoxylon australica, in the Talbragar material. Two instances where a cone and leaves are attached to a stem apex establish their relationship beyond doubt.

The Pentoxylaceae, an extinct group of arborescent cycads, similar to the Bennetitales, grew as small trees. In India their male flowers have been shown to be crown-like rings of filiform sporangiophores. Two groups of immature sporangiophores occur in the Cullen Collection. A mature sporangiophore found in a specimen from another collection, completes our knowledge of *Pentoxylon australica*.

The relative proportions in which the species are found at Talbragar, and our knowledge of the nature and appearance of the plants concerned, makes it possible to reconstruct the environment 150 million years ago when the fish beds were being laid down.

A picture emerges of a lake in an *Agathis* kauri-pine forest. Interspersed among the *Agathis* trees in the Jurassic forest were podocarpaceous conifers, and the understorey was *Pentoxylon australica* growing as small trees. The heath zone round the lake was occupied by pteridosperms—*Pachypteris pinnata* and *P. crassa* (*Thinnfeldia* spp. of Walkom), and ferns grew in rock cracks and suitable areas. There were occasional non-

arborescent cycads growing in the forest as *Macrozamia* does today, and there were cicada-like insects making a stridulating sound. The climate was probably montane 'dry rain forest'.

The remnants of kauri-pine forest which exist in Australia today are mainly on the Atherton Tableland in Queensland. Near Mt Windsor where kauri is still being logged, it forms almost pure stands on the ranges and favours western slopes in the montane dry rain forest facies and interspersed in true rain forest as well. At Thornton Peak, where it dominates the forest crown, the arborescent cycad *Lepidozamia hopei* growing with it reaches 40 feet in height, with interspersed *Podocarpus*—the same sort of assemblage of plants as at Talbragar in the Jurassic age.

The distribution of *Agathis* in the modern world is significant. The relic floral occurrences in rain forest in Queensland are remnants of the Tertiary flora which extended from northern Queensland to Tasmania. The genus occurs as well in the eastern Pacific, from the Philippines to New Zealand and from Malaysia to Fiji. It is regarded as a southern genus, the spread to localities north of the equator being relatively recent. Therefore the proof that it was established in Australia in the Jurassic, where it presumably evolved from a Gondwana ancestor, is particularly significant.



Top left, staff of the New South Wales Geological Survey 1878 with Charles Cullen, the official collector standing in the back row, far right. Photo courtesy the Geological and Mining Museum.

Top, impression of 'Conites' one of the *Carnoconites* fruits (natural size).

Above, a latex cast from the 'Conites' impression.

CLIMATE AND AUSTRALIAN FLORA

by Peter Kershaw



Wet sclerophyll forest on Mt Donna Buang, Victoria. Eucalypts are invading *Nothofagus* rainforest which is reduced to a patchy understory. Photo Peter Kershaw.

Rainfall, temperature, altitude and latitude are among the factors which contribute to the characteristics of flora and vegetation. In an island continent as vast as Australia the influence of climate on plant forms and characteristics must necessarily vary. Peter Kershaw, senior lecturer in geography at Monash University has recently been involved with vegetation history of Quarternary and Tertiary deposits in southeastern Australia. Some fascinating facts are revealed in this article in which the author underlines the need for more research to reinforce knowledge of how to conserve Australia's unique flora and vegetation.

A large number of climatic factors influence the nature and distribution of individual plants and floral associations within Australia. On this largely arid continent, precipitation plays a dominant role and there is a general change in floristic composition and structural appearance of vegetation along the decreasing rainfall gradients from coastal areas inland.

Rainforest, which can be as floristically diverse and structurally complex as any vegetation in the world, is found as isolated patches along the east coast particularly where mean annual rainfall exceeds 1400-1500mm. With reduced rainfall rainforest gives way to a large variety of sclerophyll forests and woodlands, generally dominated by *Eucalyptus* species, and these communities in turn are replaced by extensive *Acacia* shrublands in the dry interior. Although these different vegetation types have major floristic differences, it is structural characteristics which give each a characteristic appearance. For example, leaf size is controlled largely by climate and many related species show a gradual reduction in size along moisture gradients.

The effects of temperature variations are less well marked although rainforest suffers severe losses in numbers of species and structural life forms with increasing latitude. Whereas in tropical forests there may be in excess of 100 tree species per hectare in addition to many robust vines, ferns and orchid epiphytes, palms and aroids, cool temperate forests can be dominated by one tree species—Antarctic beech, *Nothofagus*—with a few attendant wiry vines, ferns and mosses.

Some latitudinal variations result also from seasonal differences in rainfall. Grasslands, the tree communities with grassy understoreys are more commonly associated with summer rainfall regimes while heathlands and low shrublands, including saltbush shrublands, characterise large areas with predominantly winter rainfall. Heathlands achieve maximum expression in parts of southwestern Western Australia and southeastern South Australia that experience very seasonal 'Mediterranean' type climates.

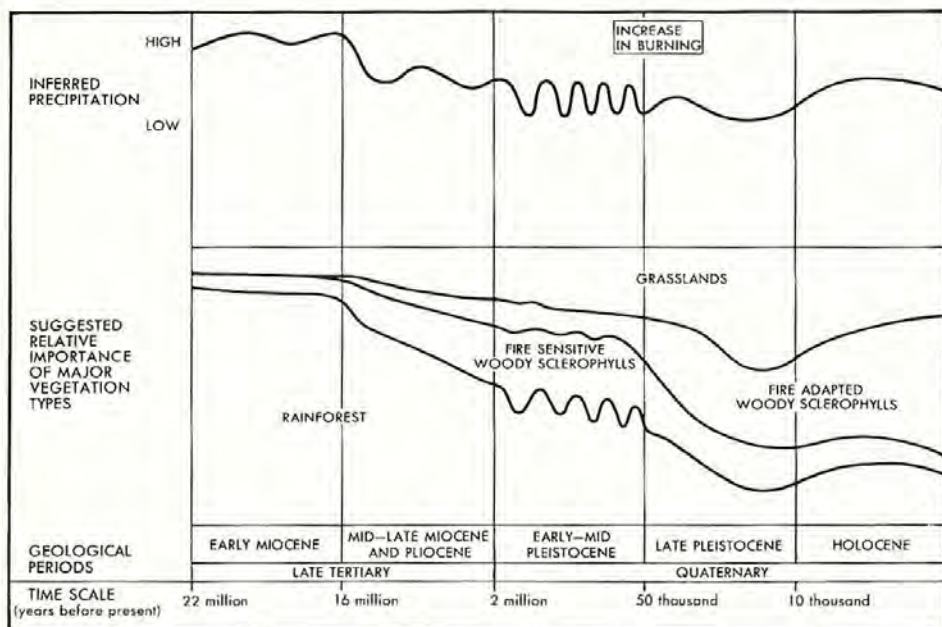
Despite these general relationships between climate and vegetation, only in a few cases has it been possible to isolate and explain those attributes of climate that determine species distributions or are responsible for the position of a vegetation boundary. One

example relates to the altitudinal tree line that appears to approximate the 10°C isotherm for the warmest month. Throughout the world trees give way to low growing shrubs or grassland at this point. In Australia it is the eucalypts snowgum, *E. pauciflora*, and *E. coccifera* that generally form the tree line in the southeastern highlands and Tasmania respectively.

Although relating to the 10°C isotherm, some recent studies suggest that the limiting factor to tree growth is not heat energy as such but a growing season too short for new growth to ripen sufficiently to withstand low temperatures and desiccation in the winter months. A more specific example concerns the limits of the important timber species karri, *Eucalyptus diversicolor*, in Western Australia. The species is widespread in areas receiving more than 100-130cm of rain a year but the actual limit for extensive stands within this range is determined by the seasonal distribution of the rainfall.

The relationship between climate and vegetation is complicated by other environmental factors. The influence of soils is expressed strongly where extensive areas of grassland and saltbush shrublands cut across the dominant zonal vegetation pattern. Grasslands tend to occur on heavy nutrient-rich alluvial soils of internal drainage basins where woody plants have difficulty in establishing. Saltbushes are succulents which inhabit soils too saline to allow the survival of most other plants. At a more detailed level of investigation, soil variations combine with other factors such as fire, topography and grazing to produce complex floral patterns which are often extremely difficult to unravel and explain. But, taking all these variables into consideration, information is still inadequate to allow understanding of the nature, composition and distribution of many vegetation types and the distribution of individual species.

Why are the acacias and eucalypts so successful? Why do *Acacia* communities, which are largely restricted to the arid zone, also occur as extensive, yet isolated patches, in high rainfall areas of northeastern Australia? How is it possible for isolated patches of rainforest to have similar floristic makeups? Why are there plants like hoop pine, *Araucaria bidwillii*, and Antarctic beech with very disjunct distributions? Questions like these can only be answered by delving into the past. Climate of the present day is simply one of a large number of climatic patterns that have con-



Top left, summary of suggested precipitation and vegetation changes through the late Cenozoic. The period is characterised by decreasing precipitation and increasing climatic variability that has caused a general reduction in rainforest at the expense of sclerophyll forests, woodlands, shrublands and also grasslands. Fire adapted sclerophylls became more important with an increase in burning around the time that aboriginal man entered the continent.

Top right, hoop pine and Antarctic beech are two large rainforest trees with restricted and disjunct distributions. Hoop pine occurs as an emergent of some rainforest communities in southern and northern Queensland. Antarctic beech is the dominant tree of rainforests in southern Victoria and Tasmania but also occurs in high altitude forests of northern New South Wales and southern Queensland.

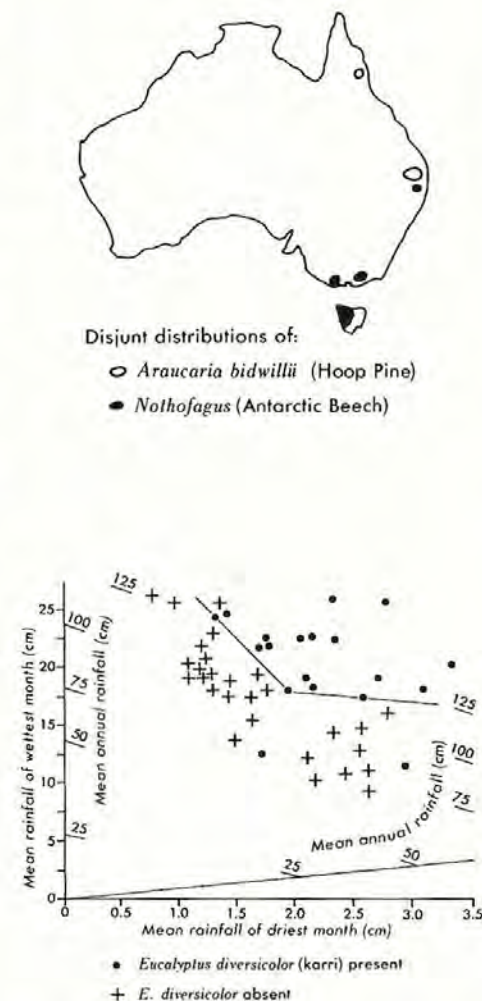
Above left, *Pittosporum* is one of a large number of genera whose leaves become progressively smaller under drier conditions.

Above right, karri is an important timber tree which is restricted to high rainfall areas of southwestern Western Australia. Its actual extent appears to be controlled by the amount of rain received in the driest month within a mean annual rainfall range of 100-150cm. From Churchill, 1968. *Aust. J. Bot.* 16:125-51.

tributed to the moulding of the vegetation landscape.

In the past there have been gross temperature changes for the Australian region on three different timescales. The two longer records are derived from studies on the fossil shell remains of small marine organisms called foraminifera. These shells are preserved in accumulating deep sea sediments and retain information about conditions at the surface of the sea where they were originally formed. The general pattern of temperature changes on dry land is assumed to have been similar to that determined for the sea surface. The third record is derived mainly from studies of pollen preserved in lake and swamp sediments within Australia itself. Pollen grains are blown into such sites where they accumulate and provide a record of the vegetation. Climatic changes are inferred from changes in the composition of the vegetation through time.

In all fossil records from the Australian region there is a close relationship between temperature and precipitation levels. This is partly because evaporation from ocean surfaces increases with temperature. When seas are warm, there is a great deal of atmospheric moisture available to form precipitation on land. During cold periods precipitation is reduced, not only because of lower evapora-



tion rates, but also because of lower sea levels, due to an accumulation of ice on Antarctica and temperate latitudes in the northern hemisphere, resulting in an increase in the area of land relative to that of the oceans.

Pollen evidence from a number of sites suggests that during the early Miocene, mixed rainforest, existing under high precipitation, covered much of Australia as it had for many millions of years. There is some evidence for the presence of grasslands associated with rainforest in the very centre of the continent but sclerophyll vegetation, including the eucalypts, must have been very restricted or not yet in existence at this time.

Environmental changes in the mid Miocene initiated trends towards the development of the present floral pattern. Decreasing precipitation caused a contraction of rainforest to coastal areas while a steepening of the temperature gradient from the equator to the south pole resulted in the latitudinal contraction in the range of many rainforest plants. These trends are well illustrated from the history of two rainforest plants, holly, *Ilex* and huon pine, *Dacrydium*. Both had very extensive and similar distributions within Miocene mixed forests but today *Ilex* is restricted to tropical lowland rainforests of northern

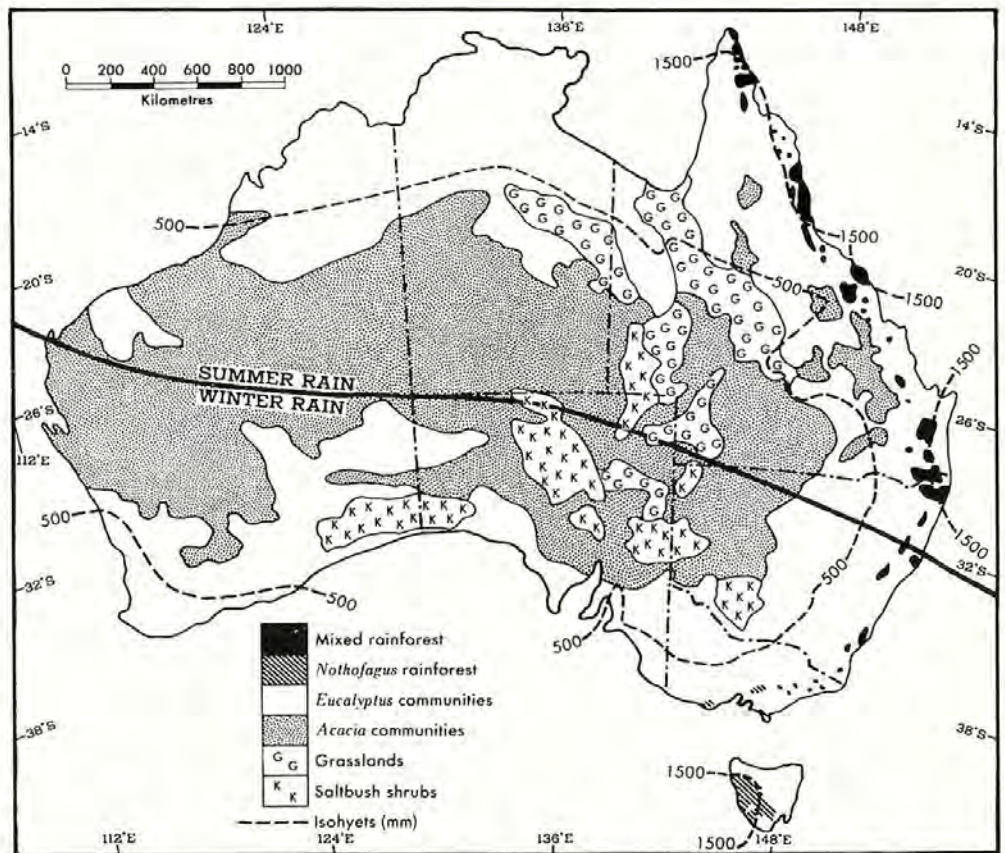
Australia and *Dacrydium* occurs only in the cool-temperate forests of Tasmania.

There is not a great deal of information on the nature of drier vegetation types that replaced the retreating rainforests as low rainfall is not conducive to the production of lake and swamp deposits within which pollen grains are best preserved. Grasslands and saltbush shrublands certainly expanded as they did in other parts of the world. Of the more characteristic Australian sclerophyll plants, she-oak, *Casuarina*, cypress pine *Callitris* and *Acacia* became more prominent but there is no evidence at this time for extensive eucalypt communities. It is possible also, that a number of drier rainforest communities such as deciduous vine thicket, which now occur in small pockets throughout the northern part of Australia down to about the 500mm isohyet, evolved or expanded in response to decreasing rainfall.

The other major event of the mid-Miocene was the establishment of contact between Australia and south-east Asia, which itself may have caused some climatic deterioration by changing oceanic and atmospheric circulation patterns. It also had the effect of allowing some mixing of the floras of the two regions. Although a large scale invasion of Australian rainforests by south-east Asian plants has often been postulated, there is little fossil evidence to support this view. The major elements of Australian rainforests were here long before this contact was made. Only in New Guinea, which forms the northern part of the Australian continental plate, is the Asian influence apparent. Invasion here was facilitated by the emergence from the sea of new land as a result of orogenic activity at the plate margin.

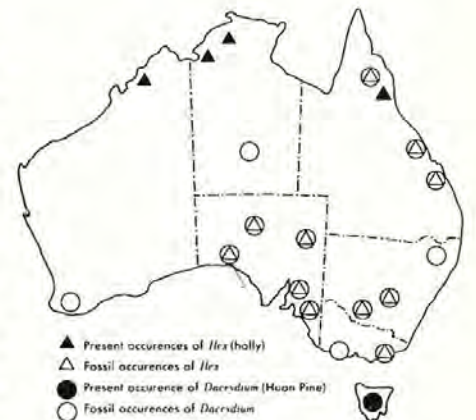
The contraction of rainforest took place gradually through the late Tertiary and by the end of the Pliocene was still more extensive than it is today. Despite a lack of fossil evidence it is thought that existing trends accelerated with increased climatic variability during the Quaternary. Deep sea core data indicate the presence of a number of 'glacial-interglacial' cycles during the last 700,000 years at least, when both temperature and precipitation fluctuated markedly. During each cool dry period rainforest would have contracted and perhaps have been unable to expand to its previous extent with the onset of favourable conditions. Sub-alpine and alpine grasslands and herbfields would have developed during 'glacial' periods. Plants which evolved from the existing flora could have been supplemented by outsiders that 'island-hopped' from one mountain peak to another through south-east Asia and northern Australasia when forest vegetation retreated in response to cool conditions.

The general pattern of floral changes probably stabilised in relation to regular climatic fluctuations until the last 'glacial-interglacial' cycle when there is evidence of major evolutionary changes in the vegetation with an increase in the frequency of fire. Aboriginal man arrived in Australia during this period and it seems likely that he was responsible for dramatic changes in fire regimes. One major change was the replacement of drier

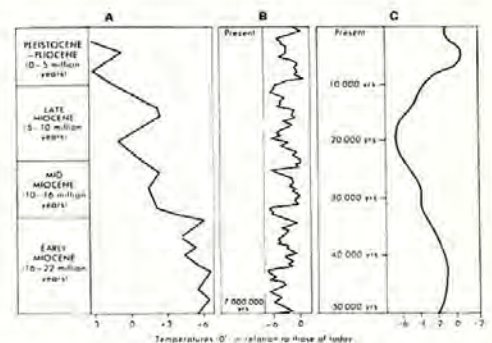


Above, some major features of the present Australian vegetation and climate.

Right, holly and huon pine illustrate the contraction in range of rainforest plants in the late Cenozoic. Fossil remains of the two plants are found together in many sites throughout Australia but through decreasing rainfall and increasing climatic variability, they now have restricted distributions in coastal rainforest patches. An increase in the temperature gradient has separated the plants latitudinally so that holly is now confined to tropical forests and huon pine to cool temperate forests.



Bottom, temperature variations in the Australian region on three time scales. A. Late Cenozoic sea surface temperatures derived from studies of fossil marine animals. From Shackleton and Kennett, 1975. *Initial Reports of the Deep Sea Drilling Project*, 29:743-755. B. Mid and late Quaternary sea surface temperatures. From Shackleton and Opdyke, 1973. *Quaternary Research* 3:39-55. C. Generalised latest Quaternary temperatures from fossil pollen evidence.





The treeline on Mt Kosciuszko. Trees of snowgum give way rather abruptly to alpine grasslands and herbfields. Photo G. Werren.

rainforest types by sclerophyll vegetation dominated by *Eucalyptus* and *Casuarina*. This change took place between 38,000 and 26,000 years ago when rainforest would have been under stress from decreasing temperatures and rainfall and the influence of fire. Once established, sclerophyll vegetation was able to be maintained under higher rainfall levels in the last 10,000 years. Drier rainforest types now only exist in local fire-proof pockets such as stream gullies and rocky outcrops. At Lake George near Canberra there is evidence for a similar decline in rainforest elements and also *Casuarina* at the expense of *Eucalyptus* with increased burning. Major changes here though are associated with an earlier high rainfall phase which was necessary for the production of sufficient plant litter to fuel intense fires.

The overall picture, gathered from these fossil records, is of a great expansion of fire-tolerant or fire-promoting vegetation at the expense of fire-sensitive types. Eucalypt forests and woodlands, in particular, were greatly advantaged and spread to dominate a large proportion of the Australian environment. Drier rainforests and a number of sclerophyll communities such as *Casuarina*, *Callitris* and perhaps *Acacia* forests were severely depleted. The actual extent and timing of major vegetation changes would have varied from region to region depending on the nature of the existing vegetation and the presence of climatic conditions conducive to the spread of fire. The major features of the vegetation landscape, including numerous species and community disjunctions, are largely a product of these relatively recent events in Australia's history.

There is a great deal of fossil information available for the last 25,000 years which has allowed vegetation and climatic reconstructions of a more detailed nature than for previous periods. At the height of the last 'glacial', 25-10 thousand years ago, open herbaceous communities were extensive and

all forests and woodlands, including those dominated by *Eucalyptus*, had very restricted distributions. On the Atherton Tablelands grasses dominated areas now covered by complex rainforest and the legacy of this period is still evident within rainforest areas. The 'grass balds' of the Bunya Mountains in southern Queensland probably provide the best example of relict grasslands within rainforest which have probably been maintained by Aboriginal burning in more recent times.

Much of southeastern Australia was covered in a distinctive grass and low shrub vegetation formed from a mixture of alpine plants that spread from the highlands under low temperatures and semi-arid species that spread from the centre in response to decreasing rainfall. It is estimated that mean annual temperatures were up to 6°C colder, and mean annual precipitation less than half that of present, in some areas.

From 15,000 years ago there is evidence of some climatic amelioration but expansion of trees from retreats is not seen until some 5,000 years later. The present climatic regime has been in operation for only the past 10,000 years and this period of time appears to have been insufficient for the establishment of stable floral assemblages. Rainforests migrate extremely slowly and it has been possible to identify retreat areas containing species which have still only marginally extended their ranges in the last 10,000 years. Hoop pine, a component of moist rainforests in north Queensland, is still restricted to refugia occupied during the dry period.

Recent climatic events may not only have been responsible for changes in the distribution and composition of vegetation communities but may also have assisted in the development of new community types. Wet sclerophyll forest, characterised by mountain ash, *Eucalyptus regnans*, which is the largest flowering plant in the world, is probably of recent origin. It enjoys similar climatic con-

ditions to rainforest but requires fire for its regeneration. Under existing fire regimes it is expanding at the expense of rainforest in southeastern Australia.

It is difficult to imagine that rainforest could have survived very dry periods in the face of this kind of competition. Therefore it is suggested that wet sclerophyll forest evolved within the last 10,000 years and was able to take advantage initially of areas denuded of forest vegetation during the preceding dry period.

A knowledge of the pattern of past climatic changes allows some prediction of the nature and timing of future events. The present, perhaps rather surprisingly, is a time of relatively high rainfall and, unless man's influence on climate increases substantially, a deterioration towards another 'glacial' period can be expected within the next few thousand years. Apart from purely economic consequences, such a change could be disastrous to rainforest and many other vegetation types, already under threat from fire and other activities of man. If the genetic resources of these ancient communities are to be preserved, informed management policies will have to be implemented. In particular, conservation reserves need to be designed to include retreat areas that presently contain maximum floristic diversity and may provide the only suitable habitats that will ensure survival in the long term.

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PROTEACEAE IN FOCUS

The family Proteaceae, apart from being one of our oldest recognisable plant families, is also shared with South America and Africa dating from the time when those continents were joined into what was known as Gondwanaland. Members of the family show a considerable range of flower and fruit types, each adapted to the differing features of the environment in which they now occur. With this selection of photographs, Surrey Jacobs, as photographer, has expertly captured the vibrant colours, characteristic shapes and familiar textures of a family which is immediately recognisable to most Australians.



Right and above, the striking inflorescence of the waratah, *Telopea speciosissima*, has received recognition as the floral emblem of New South Wales. The generic name, *Telopea* is reputedly derived from an Aboriginal word meaning 'seen from afar'. The inflorescence is made up of numerous small red flowers surrounded by large red bracts. *Telopea* is bird pollinated.

Top, a less common view of the waratah. When the flowers are pollinated they develop into thick leathery pods containing several seeds.





Above, the menacing, fruiting inflorescences of *Banksia serratifolia* were May Gibb's model for the 'Big Bad Banksia Men' of Bib and Bub fame. The seeds are retained in the woody fruits arranged along the central flower axis and surrounded by the remains of the dried flowers. The fruits open after drying out, either over a long period or after a fire.



Top left, the inflorescence of the aptly named firewheel tree, *Stenocarpus sinuatus*, acts like a beacon in rainforests to pollinating honeyeaters. The firewheel tree is a recent representative of a genus that has been present in Australia for at least 80 million years.

Left, *Banksia ericifolia*, is one of our more common eastern species of *Banksia*. This species grows rapidly from seed after a fire, storing numerous seeds in closed woody fruits borne on a woody axis. The seeds are released after fire starting the cycle again.

Right, *Banksia coccinea*, produces one of the more spectacular flower heads of this genus named in honour of Sir Joseph Banks. Like the waratah, the flower head of *Banksia coccinea* consists of numerous flowers but, unlike the waratah, the flowerhead is not surrounded by striking bracts. *Banksia coccinea* is native to Western Australia and pollinated by some of that State's honeyeaters.





This night-time scene of a raging, uncontrolled bushfire is familiar to all Australians, especially during the long summer months. While many Australian plant species survive and reproduce after such fires some plants actually depend on frequent burning for their long-term survival. Photo M. McFadyen, courtesy NSW National Parks and Wildlife Service.